Functional Response of Terrestrial Predators

TECHNISCHE
UNIVERSITÄT
DARMSTADT

Vom Fachbereich Biologie der Technischen Universität Darmstadt
zur
Erlangung des akademischen Grades
eines Doctor rerum naturalium
genehmigte Dissertation von

Dipl.-Biol. Olivera Vucic-Pestic
aus Frankfurt

Berichterstatter (1. Referent): PD Dr. habil. Ulrich Brose
Mitberichterstatter (2. Referent): Prof. Dr. Stefan Scheu
Tag der Einreichung: 19. Januar 2010
Tag der mündlichen Prüfung: 19. März 2010

За моју фамилију

(Für meine Familie)

Table of Contents

Niemand bestreitet die Wunder der modernen Wissenschaft. Jetzt wäre es an der Zeit, dass sie auch für ihre Monster die Verantwortung übernimmt.

Jakob von Üxküll (1864-1944) dt.-schwed. Biologe und Begründer der Umweltforschung

1. Overview

1.1. Background

Human activity has a profound impact on almost all terrestrial ecosystems of. Climate change is predicted to alter dramatically the temperature and precipitation patterns at all latitudes, and anthropogenic impacts such as pollution or poor ecosystem management result in widespread perturbations of native ecosystems. In order to minimise the impact of anthropogenic perturbations on ecosystem stability and function, it is of crucial importance to understand how perturbations or in a broad sense long lasting biotic and abiotic changes influence the structure of natural communities and which parameters are pivotal for preventing a collapse of the system.

The structure of natural communities is mainly determined by predator-prey interactions. The different predators and preys are linked in these communities via trophic interactions, and the outcome of these trophic interactions are a major determinant of the population-dynamics of the co-occurring species, and thus of their contribution to ecosystem function. Predator and prey populations are rarely at an equilibrium state, and natural communities are subject to important fluctuations of predator and prey populations. These fluctuations are caused by both, abiotic factors such as seasonal weather conditions, and direct consequences of trophic consumer-resource interactions. In most cases, despite these fluctuations, the populations can persist locally for long time periods. However, fluctuating populations can result in an increased instability of the community and even in extinction events, with, in some cases, dramatic consequences for the stability of the whole system.

One aspect of this work was to investigate how habitat destruction and climate change may affect predator-prey interactions and consequently the community structure in terrestrial ecosystems. Various abiotic and biotic factors determine the predator-prey relationship in terrestrial ecosystems, and the interaction strength between a predator and its prey depends mainly on the prey abundance and on the predators efficiency of resource acquisition. Thus, we investigated the impact of habitat structure on this interaction. Structured habitat can reduce the predation pressure by reducing the encounter rate between predator and prey, and by providing refuge space accessible for the prey but not for the predator. The metabolic rates of invertebrates increase with temperature, and raising global temperatures may not only lead to changes in the habitat structure, but also affect the predator-prey relationship by modifying the energetic requirements of both species. In order to understand and predict the effect of global warming on complex communities, we established sets of empirical data on the base of single predator prey interactions on fixed and varying prey densities.

Not all organisms are interacting with each other. The predators prey range is dependent on predator size, and we investigated the body-mass ratio between predator and prey as a predictor of the interactions strength in soil communities of terrestrial litter layers.

The underlying question while investigating population dynamics of predators and prey is to understand the impact of various sources leading to changes in the underlying dynamics and further to understand the roles of random and deterministic processes in population regulation. Empirical and theoretical ecologists have worked on gaining insights about the factors influencing population dynamics (Hassell and May 1973; Holling 1959a; Holt and Polis 1997; Kareiva et al. 1990; Rosenberg et al. 2005; Roughgarden 1975; Smith 1963) and food web structures (Abrahams et al. 2007; Brose, Williams, et al. 2006; Brown et al. 2004; Crawley 1992; Ginzburg and Akcakaya 1992; Hairston and Hairston 1997; Hassell 1978; May 1973; McAllister et al. 1972; Murdoch 1975; Peters 1983; Williams and Martinez 2000).

The main goal of these studies is to achieve a profound mechanistic understanding of these processes, which enables ecologists to make realistic predictions of the magnitude and the direction a system is expected to change after perturbations, species extinction or long lasting abiotic changes. Better understandings of the mechanisms driving population dynamics and species coexistence is essential and will enable us to predict and deal with the ongoing global change and its consequences on ecological systems and further more on human well-being.

In the next paragraphs, I will first introduce what food webs are, give an example of food web models, factors affecting interactions, metabolic and foraging theories, considerations about predator-prey body mass ratios, generalist predators functional response models and a summary of investigations on functional responses. Finally I will give a brief introduction in methods investigating them. Then I will provide a layout of my thesis.

1.2. What are food webs?

Food webs are the description of “who eats whom” in natural communities. They help picture how a community is put together and how the energy fluxes are distributed among the species in these communities. They represent feeding (or trophic) interactions among co-occurring species within a certain habitat or ecosystem. Despite the extreme complexity and variability of food webs, their structure possesses common characteristics, like that consumers prey generally on smaller prey and that consumption on a resource level leads to decreases in resource biomass and increases in consumer biomass or that allometric scaling enhances stability (Bersier et al. 2002; Brose, Williams, et al. 2006; Cohen et al. 1993; Solow and Beet 1998). However, to obtain satisfying descriptions of real ecosystems, natural food

webs first have to be resolved to their species composition, occurring links among the trophic levels, the interaction strengths between species, their production rates. With increasing high quality data from experimental studies and computational power stochastic and deterministic food web models evolved investigating general principles that determine the interaction strengths and energy fluxes from individual to population level. The feeding links give a description of the biomass transfers from one population level to another, including all possible trophic strategies like detritivory, herbivory, predation, cannibalism and parasitism. Ideally food web models represent whole communities, ranging from primary producer species such as autotrophic plants to higher consumer species like top predators, with all other trophic levels in-between. These models can be compared to real food webs and simplifying the relationships to tractable terms allows scientists to uncover general principles that determine interaction strengths and factors affecting and influencing the stability of predator-prey dynamics.

1.3. Food web models

In the following I will give a brief example how increased and improved understanding of the importance of body masses, link and degree distributions, niche widths of consumption and evolutionary foraging adaptations extends theoretical food web models. Conventional models used to describe food webs are e.g. the cascade model (Cohen and Newman 1985), niche model (Williams and Martinez 2000) and the nested hierarchy model (Cattin et al. 2004).

The cascade model assumes that in food webs species are ordered in a trophic hierarchy such that a given species can only prey on those species one trophic level below it and can be preyed on by only those species one trophic level above it in the hierarchy. The niche model extends the cascade model by constraining species to consume a connected sequence of prey in a one dimensional niche. Both models are based on the ecological niche concept, where the consumers are organised along one niche dimension. The underlying hypothesis of the nested hierarchy model is that any species' diet is the consequence of phylogenetic constrains and adaptation. Thus, in this model the consumers are organized in groups forming a nested hierarchy, which accounts better, in contrast to the first mentioned models, for the multidimensionality of natural ecosystems.

All these models have in common that they describe binary feeding relationships between species in a community and that they are parameterized by using diversity (the number and relative abundance of species in a particular habitat or ecosystem) and connectance (the proportion of possible links within a food web which are actually realized) to determine other descriptors.

Scientists have worked to gain insights in population and food web dynamics by isolating predator-prey interactions, or in a broader sense consumer-resource interactions, and elaborating algorithms describing the observed dependencies (Abrams 1990; Hassell et al. 1976; Hassell 1978; Holling 1959a; Martinez 1992; Murdoch and Oaten 1975; Peters 1983). Applying these algorithms to real or simulated food webs, allows drawing conclusions wether they are increasing or decreasing the stability of the investigated systems (Berlow et al. 2009; Brose et al. 2008; Brose, Jonsson, et al. 2006; Otto et al. 2007; Paine 1966; Petchey et al. 2008). These complex model simulations have improved our understanding of for example how allometric scaling provides stability in food webs (Bersier and Kehrli 2008; Brose 2008; Brose, Jonsson, et al. 2006; Otto et al. 2008, 2007), of how predator and prey traits like e.g. habitat choice influences predator-prey dynamics (Abrahams et al. 2007; Lima 1998; Peckarsky et al. 2008; Solow and Beet 1998; Stephens and Charnov 1982) or of how warming might affect population stability (Rall et al. 2008).

Based on these previous results, the aim of this thesis is to uncover general principles shaping the nonlinear interaction strengths of predator-prey interactions, so that the knowledge of predator and prey masses allows us to predict the functional response of predator-prey pairs without necessarily investigating each possible foraging interaction separately in the laboratory or in the field. Integrating these general functional response models into food-web models allows making realistic predictions about how an interaction might be changed as a consequence of changes in habitat structure, species composition, body-size structure or temperature.

1.4. Factors affecting interactions

Although the densities of both predator and prey are affected by many indirect interactions based on biotic and abiotic factors, they influence each other predominantly via direct interactions, where predation appears to be the most obvious one. Predation has been suggested as an important factor in population regulation since some forms of predation may lead to food web stability (Hassell 1978; Kondoh 2003; Murdoch 1975; Rall et al. 2008; Real 1977; Yodzis and Innes 1992).

Nonlinear trophic interactions with density-dependent predation (Hassell et al. 1977; Rall et al. 2008) are of ecological interest, because the increasing predation risk can result in a top down control (Gentleman and Neuheimer 2008) while preventing unstable boom burst population dynamics, as observed for density independent predation rates (Hassell 1978; Oaten and Murdoch 1975). If stability exists despite density independent predation, there must be other factors influencing the population dynamics (Murdoch 1975). Other factors influencing prey population may be non-consumptive effects of predators which are defined

as changes in prey traits over time (Peckarsky et al. 2008). Changes in prey behaviour can be e.g. predator induced diel vertical migration (von Elert and Loose 1996) or predator avoidance in the habitat choice of the prey (Abrahams et al. 2007; Lima 1998) which may not only result in lower consumption rates of the predators but also in lower reproduction rates of the prey, due to increased energetic expense of anti predator behaviour (Dawidowicz and Loose 1992). Another form of protection against predation is given by chemically inducible morphological changes in the prey (inducible defence mechanisms) as it is often reported for aquatic organism like ciliates (Kusch 1993), snails (Crowl and Covich 1990), rotifers (Stemberger 1988), but mostly for cladocerans (Spitze 1992; Stenson 1987; Tollrian 1995). Predator induced changes in fecundity time (Vonesh and Bolker 2005) represent also changes in prey traits and can be counted as intimidation effects of predators on their prey. Swarming can be observed in many animal taxa e.g. birds, fish and different insect species like the dreaded migratory locust, just to mention some examples, presumably as an evolved defence mechanism against predation. In the presence of other potential prey items the predation risk of each single prey individual decreases, but the predator may also become confused (Crawley 1992; Jeschke and Tollrian 2005a) confronted with too many moving prey items, since the predator has to decide which prey item to catch.

Peckarsky et al. (2008) argued that consumption and intimidation of the prey contribute to the total effects of predators on their prey, and that characteristics of keystone consumers may differ from those of predators having predominantly non-consumptive effects. If the NCE exhibit the same signal as the consumptive does, they may be overlooked even if they can affect the magnitude, rate or scale of a prey response to predation. **Obviously numerous factors may be responsible in regulating predator and prey populations but discovering the general factors shaping predator-prey interactions may help in predicting the impact of changes in predator and prey populations.**

However, many species interactions have in common that they are driven by the need to intake energy (e.g. individual growth, production and reproduction success is closely related to energy intake) and it does not surprise that the stability of complex systems is critically dependent on the distribution of energy fluxes across the feeding links (Bascompte and Melian 2005; Brose et al. 2008; De Angelis 1975; Dunne et al. 2002; Otto et al. 2007; Rall et al. 2008). Two different approaches to this topic are used to predict the energy transfer from one trophic level to another, the metavolic theory of ecology and the optimal foraging theory, and I briefly introduce them in the following section.

1.5. The metabolic theory

The metabolic theory of ecology (MTE) is based on the metabolic processes affecting every living tissue and focuses on the overall energy flux on the level of consumer individuals (per capita consumption rates).The MTE predicts, by defining physiological constrains, the individual and total energy intake which is necessary to sustain a population. According to the MTE the per capita rates of metabolism, I_j [Js^{-1}], and ingestion, J_{ij} [Js^{-1}], of a consumer individual scales with body mass M [g] and temperature, T, as (Brown et al. 2004):

$$I_j = i_0 M_j^{b_I} e^{\frac{-E_I}{kT}} \quad (1.5.1)$$

$$J_{ij} = j_0 M_j^{b_J} e^{\frac{-E_J}{kT}} \quad (1.5.2)$$

where i_0 and j_0 are normalisation constants (with c ≈ 0.75), b is an allometric exponent, k is Boltzmann's constant (8.62 x 10^{-5} eV/K) and E [eV] is the activation energy. Thus the per capita consumption rates of consumer individuals of species i, C_i [Js^{-1}], follows a similar mass dependency as the metabolic rate does (Carbone et al. 2007). If the temperature is negligible (because of only one temperature included in the experiments) the equations for calculating metabolic and consumption rates changes to:

$$I_i = I_0 M_i^a \quad (1.5.3)$$

where I_0 and a are constants (Brown et al. 2004).

$$C_i = C_0 M_i^b \quad (1.5.4)$$

where C_0 and b are constants (Carbone et al. 2007).

Implementing these relationships into individual consumer-resource feeding interactions (Brown et al. 2004; Yodzis and Innes 1992) results in a "metabolic model" that predicts energy fluxes through individual links, where the consumer's per capita consumption rate is equally distributed across all of the consumers feeding links. The per link predation rate is defined as the number of prey (or resource) j consumed per individual predator (or consumer) i at a given time scale. Thus, metabolic models predict that for any prey species per link and total energy fluxes are highest to its largest predators.

1.6. Optimal foraging theory

The optimal foraging theory (OFT) is built on phenomenological observations of

biological phenomena and focuses on the individual feeding links of predator and prey (Belovsky 1997; Bjorkman and Liman 2005; Charnov 1976; Cowie 1977; Kondoh 2003; Krebs 1977). The OFT focuses on evolutionary evolved traits like e.g. mean body mass or defence mechanisms of the prey species, to predict how behavioural aspects of predator-prey interactions determine the relative strength of the feeding links. The optimal foraging theory predicts, in contrast to the MTE, that per link predation rates, P_{ij} [Inds-1], follow a hump-shaped relationship with predator-prey body mass ratios, $R_{ij} = M_i M_j^{-1}$, as:

$$P_{ij} = P_{max}\left[\frac{R_{ij}}{R_{max}} e^{1-\frac{R_{ij}}{R_{max}}}\right]^{\gamma} \qquad (1.6.1)$$

where P_{max} is the maximum predation rate, R_{max} is the body mass ratio at which the maximum predation rate is achieved and γ is a scaling constant (Aljetlawi et al. 2004; Brose et al. 2008; Persson et al. 1998; Vucic-Pestic et al. 2010; Wahlström, Persson, Diehl, and Byström 2000). This phenomenological foraging model predicts increasing predation rates with body mass ratios when predators are small relative to their prey ($R_{ij} < R_{max}$), which can be explained by an increasing ability of the predators to subdue and handle prey (Aljetlawi et al. 2004). Furthermore, the model predicts decreasing predation rates with body mass ratios when predators are large relative to their prey ($R_{ij} > R_{max}$), what can be explained with a decreasing detectability and catchability of the small prey (Persson et al. 1998). Thus, optimal foraging models predict that per link the total energy fluxes peak at intermediate predator-prey body mass ratios.

Both theories are reasonable for modelling population dynamics. There is no doubt that all organisms have to intake energy to stay alive. The consumers foraging rate has to exceed the basal metabolic demands, so that the energy surplus can be investigated in growth and reproduction. Since resources are limited through multiple exploitation the consumer's competitive ability is one determining factor for the consumer's fitness. The competitive ability depends on the ability to forage on a resource as well as to overcome temporary resource depression (depending on metabolic demands) (Persson 1985). According to this, observed variations in size structure of populations can often be explained with resource dependent individual growth (Norberg 1988) and the competitive ability of the consumer species (Schoener 1983).

1.7. Considerations about predator-prey body mass ratio

To achieve a maximum surplus of energy predators have to make decisions on which prey they want to hunt. As a brief statement, every one who tried to catch an annoying fly has faced the problem of morphological constrains in catching and handling such a small "prey"

compared to the own body size. Assuming that this fly represents one of our prey species, our energetic expense for catching would drastically exceed the energy content of this small prey species resulting in a negative energetic efficiency and we would presumably starve if no other prey is available. Therefore no one would wonder that smaller predators have a smaller width of the consumption niche than larger predators and that a shift in targeted prey size is attended towards greater prey with increasing predator size, since prey and predator sizes are positively correlated (Cohen et al. 1993; Loeuille and Loreau 2005). In the same way it is clear that it requires much more energy to pursue and subdue very large prey, compared to the own body mass. Therefore it makes sense to assume an optimal body-mass ratio where the energetic expenditure for catching the prey item does not exceed the energy gain by consuming the prey item, resulting in a positive energetic efficiency.

Recent studies investigating consumption rates on either fixed prey densities or on varying prey densities included only one predator size class preying on differently sized prey species (Aljetlawi et al. 2004; Brose et al. 2008; Wahlström, Persson, Diehl, and Byström 2000), showed that despite power-law scaling of per capita consumption rates (according to the MTE), the per link predation rates follow hump-shaped relationships with predator-prey body-mass ratios (according to the OFT). A further study showed that not only the attack rates (including successful and unsuccessful attacks) follow these hump shaped pattern, but the success rate itself shows a similar pattern indicating that prey size selection could be an evolutionary adaptation to effective hunting (Gergs and Ratte 2009).

Consequently, we need to identify and characterize the nature of the factors influencing the variables of consumer-resource interactions, because of their potentially differing impact on population stability.

1.8. Generalist predators

Generalist predators exploit a wide range of prey species leading to unaffected predator abundance by changes in the population density of one single prey species. Therefore, it is reasonable to assume that the predator abundance in the field is more or less constant or varies randomly, uncoupled of fluctuations in prey density of one single prey species. Consequently the predator abundance must be affected by other regulating mechanisms. Other criteria can be for example the availability of suitable breeding sites, avoidance of predator interference or prey abundance. However, the intensity and form in which way a predator affects the prey density can vary with the prey species, in terms that a single predator may regulate the population density of one prey species and otherwise drive another prey species population to extinction. There are numerous possibilities of how generalist predators might affect the abundance of prey species like e.g. showing a fixed number or fixed proportion predation of

prey or density dependent predation. The underlying assumption for fixed number predation is that each predator kills always a constant number of prey, independent of how low the prey density is, while for the fixed proportion predation we assume that the predators consumption is unrestricted by gut size, handling or time limitation, since they always kill a constant proportion of the prey, regardless of how high the prey density becomes (Crawley 1992).

More realistic is to assume that predators are limited by their gut size, so that at very high prey densities the predator consumption reaches satiation and that at low prey densities the predation is reduced due to longer search times and decreased encounter rates of predator and prey. These assumptions are implemented in the functional response model (Crawley 1992; Holling 1959a; Murdoch and Oaten 1975)**.**

1.9. Functional response models

The term *functional response* was first formulated by Solomon (1949), and later categorized by Holling (Holling 1959a). Functional responses describe the changes in the consumption rate of a predator as a function of the density of its prey.

Functional responses are part of population dynamics. A familiar procedure to investigate predator-prey interactions, under controlled laboratory conditions, is to measure the functional response of a predator with its prey.

In the following, I briefly discuss the four most common forms of functional responses (type I-IV) and their potential impact on population stability.

Hollings disc equation (Holling 1959a) describes the most basic type of functional responses, the type II response. In this model consumption rate increases hyperbolically and satiates at high prey densities, which is due to a limited gut size that consequently limits the intake of the predators:

$$N_e = \frac{bN^{q+1}}{1 + bT_h N^{q+1}} \tag{1.9.1}$$

where N_e is the per capita consumption rate, N is prey abundance, T_h is the handling time needed to kill, ingest and digest a resource individual, b is a search coefficient that describes the increase in the instantaneous search rate, a, with resource abundance, N:

$$a = bN^{q+1} \tag{1.9.2}$$

where q is a scaling exponent that converts type II (q=0) into type III (q=1) functional responses (Rall et al. 2008; Williams and Martinez 2004). The hill exponent, h, used in some prior studies (Real 1977) is equivalent to q ($h = q + 1$).

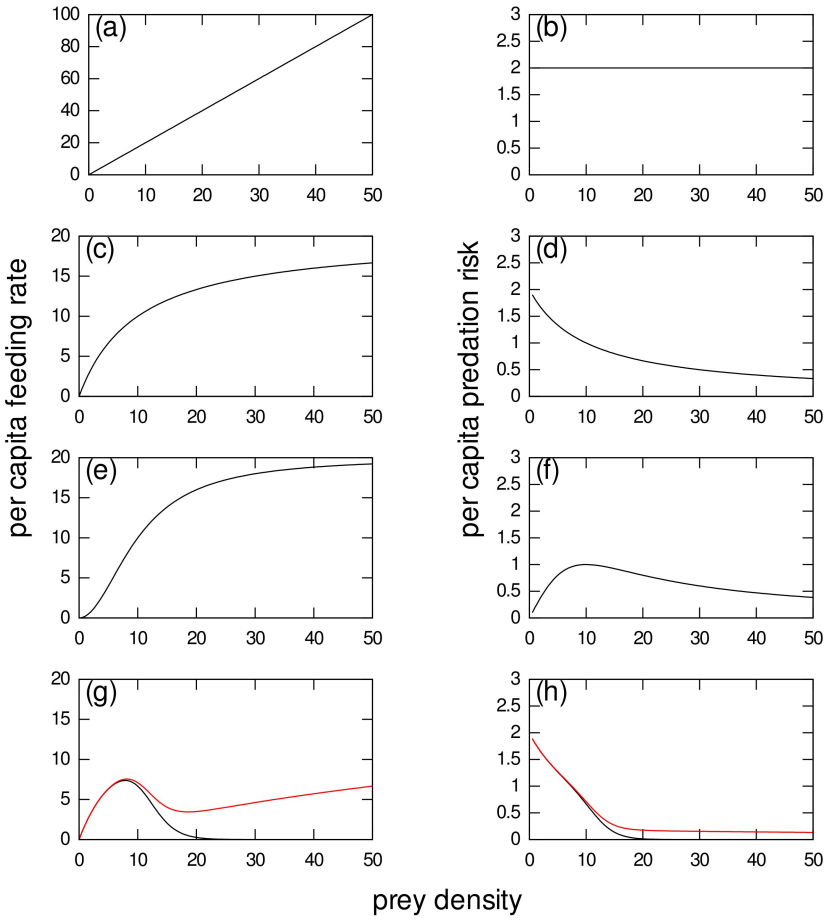

Figure 1.9.1: Functional response of predator feeding to varying prey density. (a) Type I: linear relationship between consumption and prey density results in a constant percentage kill (b). (c) Type II: hyperbolic relationship between consumption and prey density results in inverse density-dependent percentage kill (d). (e) Type III: sigmoid relationship between consumption and prey density results in direct density-dependence in percentage kill at low prey densities, but inverse density-dependence at high prey densities (f). (g) Type IV: hump-shaped (black) or roller-coaster (red) relationship between consumption and prey density results in a non-linear but inverse density-dependence in percentage kill.

For a type II functional response (q=0) a is a constant and does not change with prey density. This leads to proportionally lower consumption rates at high prey density because the percentage of prey individuals killed is inversely density dependent (Figure 1.9.1c,d). However, at infinite prey densities the predator does not need to search for prey and can spend the time available with handling the prey. Consequently, the number of prey encountered can be calculated with T_t/T_h (T_t= total time of experimental duration), assuming that the search rate is negligible. Hollings' disc equation does not account for prey depletion and overestimates the predator's consumption rate, if there is no replacement of the consumed prey

items during the experiments.

The functional response type I can be derived from Hollings type II model. If the handling time is negligible (T_h=0) the functional response becomes type I and equation (1.9.1) changes to:

$$N_e = aN \tag{1.9.3}$$

Where N_e is the number of prey consumed, a is the search rate and N is the prey density.

This model assumes a fixed proportion predation. Only if the predation shows a linear increase of consumption rate up to a certain threshold level with a sharp turning point, at which consumption remains constant, it is a functional response type I (Jeschke et al. 2004). In this model the fraction of the prey population consumed is density independent since the percentage of prey individuals killed does not change with prey density (Figure 1.9.1a,b). This model was mostly reported for the predation of filter feeders. The handling time of some filter feeders is negligible (T_h=0) because the prey is relatively small compared to the predator mass and their feeding capacity is limited only by the speed of digestion (Jeschke et al. 2004). But neither type I nor type II functional responses can lead to regulation of prey population, since the predation risk in both models is inversely density dependent. Prey regulation is only possible if the predation risk for the prey increases with prey density, in terms that the consumption rate increases at higher prey densities and is reduced at low prey densities. This criterion in fulfilled in the sigmoid model for the functional response type III (Figure 1.9.1e,f).

There are many possible equations to describe sigmoid functional responses. One equation that allows fitting both, type II and III functional responses and account for prey depletion during the experiments (contrary to Hollings disc equation), is the generalized form of Rogers's random predator equation (Juliano et al. 2001; Rogers 1972):

$$N_e = N_0(1-\exp(bN_0^q(T_h N_e - T))) \tag{1.9.4}$$

where N_e is the number of prey eaten, N_0 is the initial prey density, b is the search coefficient (search rate $a = bN_0^q$), Th is the handling time, T is the experimental duration time and q is the scaling exponent.

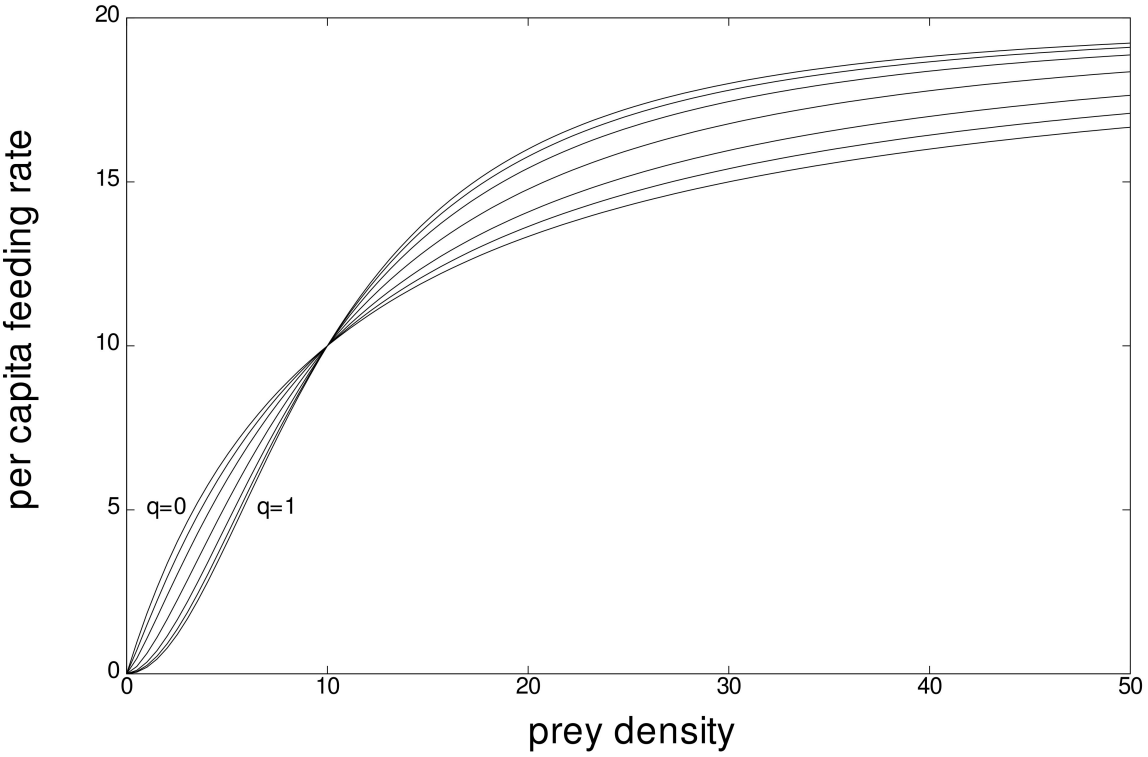

Figure 1.9.2: Different shapes of the functional response with q varrying between 0 (type II) and1 (type III).

Of course, functional responses can also become an intermediate type (Figure 1.9.2), with the scaling exponent varying between 0 and 1. The underlying assumption for the sigmoid pattern of predation is that at very low prey densities the predators are ineffective and the effectiveness increases with increasing prey density, up to maximum efficiency.

Functional response type IV shows a dome-shaped (Crawley 1992) or roller coaster (Jeschke and Tollrian 2005a) pattern of predation with increasing prey densities. Here the search rate is non-linear density dependent and can be calculated with the following equation (Bolker 2008; Jeschke and Tollrian 2005a):

$$a = \frac{e^{\varepsilon(\varphi - N_0)}}{1 + e^{(1+\beta)\varepsilon(\varphi - N_0)}}\left(\varepsilon_{max} - \varepsilon_{min}\right) + \varepsilon_{min} \qquad (1.9.5)$$

that describes a hump-shaped curve where the search rate, a, varies between a maximum (ε_{max}) and minimum (ε_{min}) value. The shape parameter β describes the increasing part of the hump, ε the decreasing part of the hump and φ is half saturation constant. It should be considered that a dome shaped functional response can become a roller-coaster functional response, if the decrease of consumption rates at intermediate prey densities is followed by a rise again at higher prey densities (Figure 1.9.1g,h).

Each of the functional response parameters is a function of several behavioural components. The characteristic components of search rate, a, are the reactive distance between predator and prey (the maximum distance at which a predator initiates an attack on its prey), the movement speed and frequency of predator and prey (influencing the encounter rate) and the proportion of successful attacks. Since larger predators have a higher visual range, the reactive distance increases with predator mass, while the proportion of successful attacks decreases with predator mass above an optimum body-mass ratio of predator and prey (Aljetlawi et al. 2004; Brose et al. 2008; Vucic-Pestic et al. 2010) and moreover the predators motivation to capture small prey of limited energy content is assumed to be low (Petchey et al. 2008).

The characteristic components of handling times, T_h, are the time a predator spends for pursuing, subduing, ingesting and digesting a prey item and any time spent resting or cleaning as a result of predation (Jeschke et al. 2002, 2004).

Obviously, the number and components building real ecosystems is infinite such as the potential number of interactions. Empirical research is therefore confined to investigate more or less simple predator-prey interactions at the individual level, limited by logistical constrains and the limited biological tractability resulting from very complex experimental designs. In most cases, laboratory studies are based on simplifying assumptions, e.g. investigation of a single predator prey interaction under controlled laboratory conditions ignores the occurrence of alternative prey or competitors in the field. Moreover it is obvious that it is impossible to simulate whole ecosystems or communities under laboratory conditions and in field experiments the factors influencing the results are often difficult tractability, since it is impossible to regulate all of them in natural systems. Simulation models are not restricted in this way and allow investigation of tractable factors influencing simple and complex systems, since the large number of equations and variables (representing empirically observed relationships as well as logical decisions and assumptions) are left to computational calculation.

1.10. Summary of investigations on functional responses

Several factors have been shown to affect the functional response of invertebrate predators of aquatic and terrestrial systems. According to the functional response models, the functional response is mainly affected by consumer traits like handling time and search rate (Holling 1959b; Jeschke et al. 2002). Allometric and metabolic theory predicts a negative ¾ power-law relationship between handling time and predator mass (Brown et al. 2004; Carbone et al. 1999; Koen-Alonso 2007; Peters 1983; Yodzis and Innes 1992). The underlying assumption is

that at infinite prey densities the search rate is negligible and thus the maximum consumption rate should be inversely proportional to handling time (Koen-Alonso 2007; Yodzis and Innes 1992). According to the ¾ power-law scaling of maximum consumption rate with body mass (Carbone et al. 1999; Peters 1983) handling time should follow a negative ¾ power law with predator mass. This trend is in principle supported, although studies reported exponential (Aljetlawi et al. 2004; Hassell et al. 1976; Thompson 1975, 1978), linear (Hassell et al. 1977; Spitze 1985) and power law relationships.

Furthermore, investigations on the effect of temperature on the functional response parameters report consistently the exponential decrease of handling time with increasing temperature (according to the MTE), but also that the scaling of attack rates with increasing temperature can be linear, sigmoid, hyperbolic, dome-shaped or absent at all (Bailey 1989; Bergman 1987; Cave and Gaylor 1989; Dreisig 1981; Garcia-Martin et al. 2008; Gilioli et al. 2005; Gresens et al. 1982; McCoull et al. 1998; Song and Heong 1997; Thompson 1978; Xia et al. 2003; Zhang et al. 1996).

Other scientists, investigating the influence of increased predator density, reported decreased per capita consumption rates due to predator interference (Beddington et al. 1976; DeAngelis and Holland 2006; Schenk and Bacher 2002; Skalski and Gilliam 2001). Predator interference reduces the time spend for searching prey and thus constrains the per capita consumption rate of predators (Elliott 2003; Vance-Chalcraft and Soluk 2005; Vance-Chalcraft et al. 2007). The hunger level and the predator's level of satiation were also shown to influence the search rate, since for relatively large prey items predator satiation occurs at each capture event and the time available for search is reduced by the relatively long handling time (attack and ingestion of the prey) and the time needed for digestion. For relatively small prey items the predation rate is continuous at low prey densities, as a result of increased search rates due to reduced handling times, while at high prey densities predator satiation occurs after the capture of several small prey items (Mills 1982; Nakamura 1974). Therefore it does not surprise that the developmental stage of predator and prey or more general the body mass ratio also plays an important role which type of functional response occurs between predator and prey (Aljetlawi et al. 2004; McArdle and Lawton 1979; Thompson 1975).

Real (1977) argued that the functional response type may change if the predator learns to exploit its prey more effective with increasing prey densities. Thus, it comes as no surprise that changes in the predators search mode (from ambush to walking) were shown to have the potential to change the functional response from type II to type III (Akre and Johnson 1979). In the same way habitat structure may influence the predators search mode. In complex habitat structure the prey can hide in refuges and the predator is restricted to catch only the

available prey items outside of refuges. When the habitat structure is very simple or does not exist at all, the prey can not hide from the predator and most of the prey individuals of the population are available to predation.

One aspect of this thesis was to investigate how differences in habitat structure influence the prey traits and affect the form of the functional response. We studied the influence of habitat structure with the intention to increase our mechanistic understanding of how the ongoing global change might affect direct or indirect the functional response parameters or predator and prey traits and consequently species coexistence and food web stability.

1.11. Studies in this thesis

In this work I focused on the impact of generalist predators on their prey and investigated how other factors like temperature, habitat structure or allometric scaling may affect these predator-prey interactions. Increasing temperature does not only change the vegetation but also the species composition. Thus warming might not only effect the habitat structure of ecosystems, it can also lead to changes in prey availability or lead to species extinction (Baulch et al. 2005; Daufresne and Boet 2007; Forchhammer and Post 2000; Hughes 2002; Mann 2007; Parmesan et al. 1999, 2000; Parmesan 2007).

In a previous study (chapter 2.1) we testes the distribution pattern of energy fluxes in dependence on body-mass ratios at constant prey densities. We compared, by calculating the energy fluxes on the population level, the predictive power of metabolic against foraging models. The influence of allometric scaling on the functional response was tested using a wide range of predator-prey body mass ratios, with 12 differently sized generalist predator species (carabid beetles and wolf spiders) and three differently sized prey types (fruit fly, beetle larvae and springtail). For more details see chapter 2.2.

We tested how the ingestion rates of arthropod predators at constant prey densities are affected by warming. The short term interaction-strengths derived from this experiments were introduced in a population-dynamic model (Rall et al. 2008; Vasseur and McCann 2005; Yodzis and Innes 1992) to calculate the long term interaction strengths of prey density, N [Ind/m²], and predator density, P [Ind/m²] (see chapter 2.3). Furthermore, I tested the influence of temperature and prey mobility on the functional response, using three size classes of carabid beetles as predators and two prey types with different moving patterns (fruitfly as highly mobile prey and beetle larvae as less mobile prey). These functional response experiments were conducted at six different temperatures ranging between 5-30°C (see

chapter 2.4).

I studied the functional responses of ground-dwelling generalist predators (carabid beetles and wolf spiders) in the laboratory. In this study I addressed the question if habitat structure constrains the detectability of prey and as consequence the predators' consumption rate. Therefore I tested the predators' functional response in experimental arenas with moss as habitat structure and without habitat structure . Additionally, I tested the prey behaviour in dependence on habitat structure (chapter 2.5).

1.12. Outline of the thesis

In chapter 2.1. we addressed the question if metabolic or foraging models predict more accurate the energy fluxes between population levels. We calculated from our experimental results, the field encounter rates and energy fluxes between predator and prey and compared the predictive power of both metabolic and foraging model. Our results show that despite clear power law scaling of metabolic and per capita consumption rates with body mass (according to the MTE), the per link predation rates for individual prey followed hump-shaped relationships with predator-prey body-mass ratios (according to OFT). Thus, in contrast to predictions of the metabolic models, our findings suggest that for any prey species per link and total energy fluxes are highest to its predators of intermediate body size than to its largest predators.

In chapter 2.2. we extended the approach of chapter 2.1., to test if our previous results are of broad generality. We studied the functional responses in dependence on allometric scaling. These scaling relationships suggest that non-linear interaction strengths can be predicted by the knowledge of predator and prey body masses and integrating these relationships into population models will allow predicting energy fluxes, food web structures and the distribution of interaction-strengths across food web links based on the knowledge of the body masses of interacting species.

In chapter 2.3. we addressed the question how increased temperatures affect ingestion and metabolic rates of terrestrial arthropod predators, and how warming affects the interaction strengths and consequently the stability of the system. We could show that warming does not only increase the metabolic requirements of the predators, but also that the temperature effects were weaker on ingestion than on metabolism. From the experimental short term per capita interaction strengths we calculated long term interaction strengths, and these predicted long term per capita interaction strength decreased with temperature. Our results indicate that on the one hand warming could increase intrinsic population stability while on the other hand decreasing ingestion efficiencies increase the extinction risk of the predators. To summarize, warming is expected to have complex and in some cases drastic effects on predator-prey

interactions and food web stability. Our approach of chapter 2.3 presents a simplistic and mechanistic null model of warming effects on predator prey interactions in which thermal adaptation effects need to be included in future studies.

In chapter 2.4. we extended the approach of chapter 2.3 to varying prey densities including the prey trait "movement pattern" into our experiments. Here we present strong evidence that warming imposes energetic restrictions on arthropod predators by decreasing their ingestion efficiency. Consequently, warming should increase stability of the populations. Our results also confirm the suggestion that warming increases the risk of predator starvation due to decreased ingestion efficiencies. The mechanistic functional response framework of chapter 2.4. may allow making detailed predictions about consequences of increasing temperature on predator-prey interaction strengths depending on metabolic and behavioural constrains.

In chapter 2.5. we investigated the influence of changes in habitat structure on the functional response and in additional experiments the prey behaviour. We show that adding habitat structure alters the functional response type II to type IV (roller-coaster). Additional experiments on the prey behaviour suggest that the decreased consumption rates at high prey densities can be explained by aggregative defence behaviour. Analysing the net energy gain of the predators in both treatments showed that with habitat structure the predators' energy net gain was limited at intermediate prey densities where prey aggregation reduced the consumption rate. Our results stress the importance of both, habitat structure and prey behaviour in shaping the functional response in soil-litter predator-prey interactions.

1.13. Conclusions

This thesis presents a mechanistic framework for making detailed and realistic predictions about the functional response type and and the distribution of the predator -prey interaction-strengths, by the knowledge of predator-prey body masses, without necessarily studying each functional response in the laboratory or in the field (chapter 2.1.and 2.2.). Further more the mechanistic framework of chapter 2.3. and 2.4. improves our understanding of how metabolic and behavioural constrains affect predator-prey interaction strengths under warming. The results present strong evidence that rising temperatures imposes energetic restrictions on arthropod predators by decreasing their ingestion efficiencies. Thus, a decrease in interaction strengths follows as consequence of the minimized ingestion efficiencies. Less fluctuations in population densities over time (due to decreased interaction strengths) should increase the population stability, but decreasing ingestion efficiencies impose also the risk of predator starvation. Since global warming alters the precipitation and temperatures in all latitudes, it leads to changes in habitat structure. Changes in habitat structure may in turn result in changes of the predators functional response type, in terms that interaction strengths

increase if e.g. a predators functional response type III (stabilizing effect) becomes of type I or II (destabilizing effect, see chapter 2.5.). However, in terrestrial systems habitat structure influences microclimate conditions leading to patchy distributions of predator and prey, according to their environmental demands. Consequently, changes in habitat structure may not only affect the species distribution in natural systems, but also affect strongly the predator prey interactions and population stability. Taken all together, our results strengthen the urgency to minimize the anthropogenic impact on the global climate and the habitat destruction of ecosystems. We still need a profound knowledge about general principles building the components of food web and population models to be able to predict changes on ecosystem stability and function as consequence of the ongoing global change. Implementing the parameters of functional response models, derived from my laboratory experiments, into population and food web models may advance our understanding of general principles driving population stability and species persistence in natural ecosystems. In this thesis I present a theoretical framework for understanding allometric and temperature scaling effects on predator-prey interactions and consequently on the stability of natural systems. However, a general understanding of temperature effects on the stability and functioning of natural systems is still lacking and further work addressing this topic is needed to fill the gap . We are now facing the problems going along with the global change and it is fundamentally important to counteract the ongoing species loss due to human induced habitat destruction and prospective to global change.

1.14. Contributions to the included articles

Chapter 2.1.: Foraging theory predicts predator–prey energy fluxes

Authors: Brose, U., Ehnes, R., Rall, B.C., Vucic-Pestic, O., Berlow, E. & Scheu, S.

Published in: Journal of Animal Ecology (2008), Vol. 77, pp. 1072-1078; doi: 10.1111/j.1365-2656.2008.01408.x

U.B., R.E., B.C.R and O.V.P. had the Idea and carried out the experiments. Statistical analyses by U.B. and B.C.R., the text was written mainly by U.B., E.B. and S.S. with minor contributions of R.B., B.C.R. and O.V.P..

Chapter 2.2.: Allometric functional response model: body masses constrain interaction strengths

Authors: Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U.

Published in: Journal of Animal Ecology (2010), Vol. 79, pp. 249–256; doi: 10.1111/j.1365-2656.2009.01622.x

Idea by O.V.P, B.C.R. and U.B., laboratory work by all authors; statistical analyses by O.V.P and B.C.R.; the text was written mainly by O.V.P. and U.B. with minor contributions of B.C.R. and G.K..

Chapter 2.3.: Temperature, predator-prey interaction strength and population stability

Authors: Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M.C. & Brose, U.

Published in: Global Change Biology, in press.; doi: 10.1111/j.1365-2486.2009.02124.x

Idea by B.C.R., laboratory work by B.C.R., O.V.P., R.B.E. and U.B.; statistical analyses and theoretical analysis by B.C.R.; the text was written mainly by B.C.R., M.C.E. and U.B..

Chapter 2.4.: Prey mobility constrains warming effects on interaction strengths

Authors: Vucic-Pestic, O., Rall, B.C., Ehnes R.B. & Brose, U.

Unsubmitted manuskript.

Idea by O.V.P., B.C.R., R.B.E. and U.B., laboratory work by all authors, but mainly by O.V.P. and R.B.E.; statistical analyses by O.V.P and B.C.R.; the text was written mainly by O.V.P. and U.B. with minor contributions of B.C.R. and R.B.E..

Chapter 2.5.: Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction

Authors: Vucic-Pestic, O., Birkhofer K., Rall, B.C., Scheu S. & Brose, U.

Submitted manuskript in Pedoboilogia.

Idea by O.V.P. and K.B., laboratory work by O.V.P., statistical analyses by O.V.P & B.C.R.; the text was written mainly by O.V.P., S.S. and U.B. with minor contributions of K.B., B.C.R..

2. Articles

2.1. Foraging theory predicts predator–prey energy fluxes

a) Summary

1. In natural communities, populations are linked by feeding interactions that make up complex food webs. The stability of these complex networks is critically dependent on the distribution of energy fluxes across these feeding links.

2. In laboratory experiments with predatory beetles and spiders, we studied the allometric scaling (body-mass dependence) of metabolism and per capita consumption at the level of predator individuals and per link energy fluxes at the level of feeding links.

3. Despite clear power-law scaling of the metabolic and per capita consumption rates with predator body mass, the per link predation rates on individual prey followed hump-shaped relationships with the predator–prey body mass ratios. These results contrast with the current metabolic paradigm, and find better support in foraging theory.

4. This suggests that per link energy fluxes from prey populations to predator individuals peak at intermediate body mass ratios, and total energy fluxes from prey to predator populations decrease monotonically with predator and prey mass. Surprisingly, contrary to predictions of metabolic models, this suggests that for any prey species, the per link and total energy fluxes to its largest predators are smaller than those to predators of intermediate body size.

5. An integration of metabolic and foraging theory may enable a quantitative and predictive understanding of energy flux distributions in natural food webs.

b) Introduction

Natural ecosystems comprise a large number of species engaging in a vast number of predator–prey interactions of variable strength (Berlow et al. 2004; Wootton and Emmerson 2005). Two categories of interaction strength most commonly studied include (1) the magnitude of energy flowing from prey to predator, or predator consumption rates; and (2) the change in abundance of one species given a change in abundance of another, or the dynamic coupling of two species. Both measures provide insight into the stability of complex food webs (Brose, Williams, et al. 2006; Montoya et al. 2006; Navarrete and Berlow 2006; Otto et al. 2007; Rall et al. 2008). Thus a critical step for moving beyond descriptive, community-specific approaches in ecology is to uncover general principles that determine interaction strengths (Berlow et al. 2004; Brose et al. 2005; Montoya et al. 2006). While not always directly related, high consumption rates (high energy fluxes) can establish the potential for strong dynamic coupling between two species (Bascompte et al. 2005; Brose et al. 2005). Here we focus on general principles that determine energy fluxes, because recent allometric models based on metabolic scaling theory (Brown et al. 2004) have proposed that predator consumption rates follow a power-law increase with predator body mass (Emmerson and Raffaelli 2004; Reuman and Cohen 2005; Wootton and Emmerson 2005; Yodzis and Innes 1992). The elegant simplicity and empirical tractability of this theory has led to its recent widespread application in theoretical studies (Brose, Williams, et al. 2006; Emmerson and Raffaelli 2004; McCann et al. 1998; Williams and Martinez 2004).

By defining physiological constraints, metabolic theory predicts the per capita (per individual) and total consumption rates necessary to sustain a population. However, being based only on predator body masses, this approach cannot distinguish the energy fluxes among the individual feeding links of generalist predators (hereafter, per link fluxes). It thus predicts per link fluxes by distributing per capita consumption rates equally across the feeding links. In contrast, foraging theory uses traits of the prey species, such as average body masses (where the average is an evolutionarily stable mean over the individuals of a population), to predict how behavioural aspects of predator–prey interactions determine the relative strength of these feeding links while ignoring the overall energy flux at the level of predator individuals. Here we propose a framework that integrates metabolic theory at the levels of predator individuals (per capita) with foraging theory at the level of feeding interactions (per link). Our focus on predator–prey energy fluxes complements recent analyses of how allometric foraging models predict food-web topology (Beckerman et al. 2006). We first introduce the models, then test their predictions using laboratory data on metabolism and consumption of arthropods. Macroecological abundance-mass relationships scale-up these predictions to natural communities with variance in predator and prey abundance.

c) Models

Per capita metabolism and consumption

At the level of individuals, metabolic theory predicts that the metabolic rates of species i, I_i [J s^{-1}], scale with body mass, M_i (g) as:

$$I_i = I_0 M_i^a \tag{2.1.1}$$

where I_0 and a are constants (Brown et al. 2004). Moreover, it predicts that per capita consumption rates of consumer individuals of species i, C_i [J s^{-1}], follow a similar mass-dependence to the metabolic rates:

$$C_i = C_0 M_i^b \tag{2.1.2}$$

where C_0 and b are constants (Carbone et al. 2007).

Per link consumption

Direct application of this per capita relationship (equation 2.1.2) to individual feeding interactions between predator i and prey j yield per link consumption rates, K_{ij} [J s^{-1}]:

$$K_i = K_0 M_i^b \tag{2.1.3}$$

where K_0 is a constant and

$$C_i = \sum_j K_{ij}$$

(Brown et al. 2004; Yodzis and Innes 1992). This 'metabolic model' predicts energy fluxes through individual links by distributing the predator's per capita consumption rate equally across its feeding links.

In contrast, foraging theory suggests that per link predation rates P_{ij} [ind s^{-1}] (the number of individuals of prey j consumed per individual of predator i) follow a hump-shaped relationship with predator-prey body-mass ratios $R_{ij} = M_i M_j^{-1}$:

$$P_{ij} = P_{max}\left[\frac{R_{ij}}{R_{max}} e^{1-\frac{R_{ij}}{R_{max}}}\right]^{\gamma} \tag{2.1.4}$$

where P_{max} [ind s^{-1}] is the maximum predation rate, R_{max} is the body-mass ratio at which this maximum is achieved, and γ is a scaling constant (Aljetlawi et al. 2004; Byström et al. 2003; Finstad et al. 2006; Persson et al. 1998; Wahlström, Persson, Diehl, and Byström 2000; Wilson

1975). This phenomenological foraging model describes (1) predation rates increasing with body mass ratios when predators are small relative to their prey ($R_{ij} < R_{max}$), which is explained by an increasing ability of the predator to subdue and handle prey; and (2) predation rates decreasing with body mass ratios when predators are large relative to their prey ($R_{ij} > R_{max}$), which results from a decreasing detectability and catchability of smaller prey (Aljetlawi et al. 2004; Persson et al. 1998).

Macroecological energy fluxes

The metabolic model (equation 2.1.3) and the foraging model (equation 2.1.4) predict laboratory energy fluxes at a fixed abundance, N'_j [ind]. This implies similar laboratory encounter rates for each prey: E'_{ij} [ind s^{-1}] = $E'_0 N'_j$, where E'_0 and N'_j are constants that are independent of body mass. In natural communities, however, field encounter rates, E'_{ij} [ind s^{-1}] = $E'_0 N'_j$ depend on field prey abundance, N_j [ind] (Emmerson et al. 2005) that scales with body mass as:

$$N_j = N_0 M_j^{-c} \qquad (2.1.5)$$

where N_0 and c are macroecological constants and often $c \approx 0.75$ (Brown et al. 2004; Meehan 2006a). Synthesizing either the metabolic model or the foraging model with this macroecological abundance–mass relationship scales up predictions from laboratory to field conditions. The per capita energy flux, F_{ij} [J s–1], through the link from prey population $_j$ to an individual of predator population i, can be derived under the metabolic model by normalizing the per link consumption rates (equation 2.1.3) by the laboratory encounter rates, E'_{ij}, and multiplying them with field encounter rates, E_{ij}:

$$F_{ij} = K_{ij} E'^{-1}_{ij} E_{ij} = K_{ij} E'^{-1}_0 N'^{-1}_j E_0 N_j = E'^{-1}_0 E_0 N_0 K_0 N'^{-1}_j M_i^b M_j^{-1} \qquad (2.1.6a)$$

This approach distributes per capita consumption rates across feeding links using encounter rates that apply to averages over individuals within populations, while ignoring differences among individuals. Under the foraging model (equation 2.1.4), F_{ij} [J s^{-1}] is equal to predation rates, P_{ij} [ind s-1] divided by the laboratory encounter rate, E'_{ij}, and multiplied by the field encounter rate, E_{ij}, and prey energy content [the product of prey mass, M_j [g ind^{-1}] and the energy content per wet mass ε [J g^{-1}] :

$$F_{ij} = P_{ij} E'^{-1}_{ij} E_{ij} \varepsilon M_j = P_{ij} E'^{-1}_0 N'^{-1}_j E_0 N_j \varepsilon M_j = E'^{-1}_0 N'^{-1}_j E_0 N_0 \varepsilon P_{ij} M_j^{1-c} \qquad (2.1.6b)$$

The total energy flux from prey population j to predator population i, T_{ij} [J s^{-1}], is defined as the product of the per capita energy flux (equation 2.1.6a or 2.1.6b) and predator abundance $N_i (N_i = N_0 M_i^{-c})$, which yields:

$$T_{ij} = E'^{-1}_0 E_0 K_0 N_0^2 N'^{-1}_j M_i^{b-c} M_j^{-c} \qquad (2.1.7a)$$

$$T_{ij} = E'^{-1}_{0} N'^{-1}_{j} E_0 N_0^2 \varepsilon P_{ij} M_i^{-c} M_j^{1-c} \quad (2.1.7b)$$

under the metabolic (equation 2.1.7a) and foraging (equation 2.1.7b) model, respectively.

d) Methods

We used ground-dwelling beetles and spiders to test these model predictions in laboratory experiments. Pitfall trapping yielded 16 carabid and staphylinid beetle species (Abax ovalis, *Abax parallelepipedus*, *Calathus melanocephalus*, *Calathus piceus*, *Carabus auratus*, *Harpalus affinis*, *Nebria brevicollis*, *Notiophilus biguttatus*, *Notiophilus laticollis*, *Ocypus olens*, *Philonthus fuscipennis*, *Platynus dorsalis*, *Poecilus versicolor*, *Pseudophonus rufipes*, *Pterostichus melanarius*, *Pterostichus oblongopunctatus*) and 10 lycosid, pisaurid and salticid spider species (*Alopecosa* sp. juv. I, *Alopecosa* sp. juv. II, *Alopecosa cuneata*, *Pardosa lugubris*, *Pardosa palustris*, *Pirata piraticus*, *Pirata latitans*, *Pisaura mirabilis*, *Salticus scenicus*, *Trochosa terricola*; for authorities see Brohmer & Schaefer 2006). The juveniles of *Alopecosa* sp. were considered as trophic species as they vary from adults in their prey spectrum. We used only adult females of the other spider species. The species chosen are common epigeic predators in central Europe.

All experiments were carried out under controlled laboratory conditions (12 h light per day, 15°C). We measured the basal metabolic rates of six individuals of each species with an automated electrolytic microrespirometer (Scheu 1992). We converted the measured O_2 fluxes (ml O_2 s^{-1}) per spider individual into energetic equivalents (J s^{-1}) by assuming that 1 ml O_2 equals 20.1 J. Prior to the consumption experiments, the predator species were fed and then starved for 5 days. All individuals were weighed before and after the experiments on a precision scale. We used the average of these weights throughout all analyses. We used collembolans (*Heteromurus nitidus*) and crickets (*Gryllus sigillatus*) as prey for the spiders, and fruit flies (*Drosophila hydei*) and fly larvae (*Lucilia caesar*) as prey for the beetles, which yielded a total of 32 and 20 predator-prey interactions for beetles and spiders, respectively. We studied predation by placing one predator individual in each arena (0.2 × 0.2 m), in which 2.35 g dry moss (*Polytrichum formosum*) was evenly dispersed as habitat structure. The moss was dried for 4 days at 60°C to exclude other animals, and was moisturised prior to the experiments. In each experimental replicate, one predator individual and 30 individuals of one prey species (initial prey density N_i) were placed in an arena, and we counted the number of prey that remained after 24 h (final prey density N_e). We used eight replicates per predator-prey combination, and calculated the energy fluxes for each replicate (K_{ij} in equation 2.1.3) by multiplying the number of prey individuals consumed ($N_c = N_i - N_e$) by the average weight of the prey individuals (g) and the energy content per mg prey wet mass (7 J g^{-1}) (Peters 1983). The use of this general energy content per mg wet mass ignores taxon-specific variation in

energy density due to difference in stoichiometry. Given that most of the variation in predator–prey body mass ratios was caused by variance in predator body masses, this generalization appears to cause a relatively small error in energy contents. The predation rates (P_{ij} in Eqn. 2.1.4) equalled the number of prey individuals consumed per individual predator. Control treatments without predators exhibited similar prey densities at the beginning and end of the experiment, suggesting that any decline in prey density in predator enclosures was due to consumption rather than natural mortality. The per capita consumption rates of the predator species (C_i in Eqn. 2.1.2) were calculated under the assumptions that the predators encounter and attack their prey by chance, and we averaged the independently measured per link consumption rates of the two prey populations [j = 1, 2; $C_i = (K_{i1} + K_{i2})/2$ or $C_i = K_{ij}$ if only j is consumed].

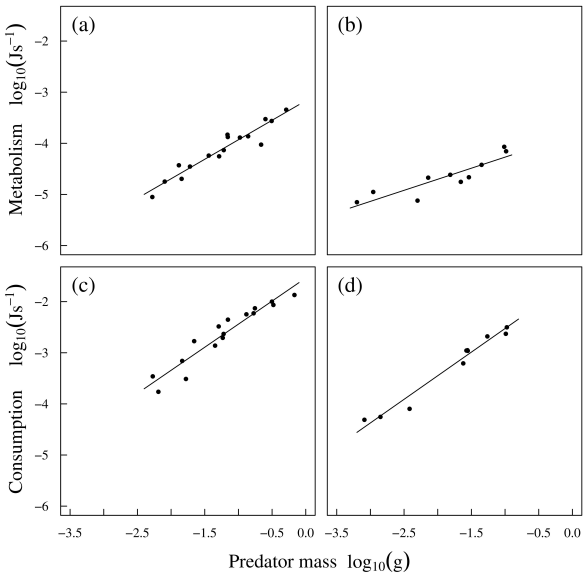

Figure 2.1.1: Laboratory measurements at the species level: metabolism, **(a)** beetles; **(b)** spiders) [$\log_{10}$ (J s^{-1})] and per capita consumption, **(c)** beetles; **(d)** spiders [$\log_{10}$ (J s^{-1})] depending on predator body mass ($\log_{10}$ g). Fitted model parameters (± SE). **(a)** Equation 1: a = 0.76 ± 0.06; $\log_{10} I_0$ = –3.17 ± 0.09; r^2 = 0.91; P < 0.0001; n = 16; **(b)** equation 1: a = 0·43 ± 0·07; $\log_{10} I_0$ = –3·84 ± 0·16; r^2 = 0.8; P < 0·001; n = 10; **(c)** equation 2: b = 0.9 ± 0.08; $\log_{10} C_0$ = –1.54 ± 0.1; r^2 = 0·91; P < 0·0001; n = 16; **(d)** equation 2: b = 0.92 ± 0.06; $\log_{10} C_0$ = –1.6 ± 0.11; r^2 = 0.97; P < 0.001; n = 10. Predator individuals were the same in upper **(a,b)** and lower **(c,d)** panels, but their body masses were slightly heavier in the lower panels because we averaged their masses before and after the feeding experiments.

We calculated the averages of the metabolic rate, the per capita consumption rate and the body mass for each predator species, and the averages of the predation rate, per link consumption rate and body mass ratio for each predator–prey interaction. The relationships between (1) average metabolic rate and average predator body mass; (2) average per capita consumption rate and average predator body mass; (3) average per link consumption rate and average predator body mass; and (4) average predation rate and average predator–prey body mass ratio were all analysed by nonlinear least-squares regressions.

e) Results

Per capita metabolism and consumption

The metabolic rates exhibited a power-law increase with the average body mass of the species, but the exponent of the relationship was higher for beetles (a = 0·76 ± 0·07; mean ± SE, Fig. 2.1.1a) than for spiders (a = 0·43 ± 0·07; Fig. 2.1.1b). The per capita consumption rates also followed a power-law relationship with the average body mass, but the slopes were steeper (Fig. 2.1.1c,d).

Per link consumption

At the level of feeding links, the metabolic model (Eqn. 2.1.3) gave a poor fit to the per link consumption rate data for beetles (Fig. 2.1.2a, r^2 = 0·39) and spiders (Fig. 2.1.2b, r^2 = 0·36). Interestingly, the per link consumption rates of large predators were higher than predicted by the metabolic model when they consumed the larger of the two prey species (fly larvae for beetles; crickets for spiders; Fig. 2.1.2a,b), and were lower than predicted when they consumed the smaller of the two prey species (fruit flies for beetles; collembolans for spiders; Fig. 2.1.2a,b). The hump-shaped foraging model (Eqn. 2.1.4) explained a much higher fraction of the variation in predation rates of beetles (Fig. 2.1.2c, r^2 = 0·60) and spiders (Fig. 2.1.2d, r^2 = 0·78). The maximum predation rates were reached at intermediate body mass ratios of R_{max} = 38·1 ± 6·2 and R_{max} = 103·1 ± 14·5 (mean ± SE) for beetles and spiders, respectively. Observations during the experiments suggest that predation was limited by the relatively long time needed to subdue and handle the prey at low body mass ratios. At high body mass ratios, predation was limited by the high escape efficiencies of prey species due to fast reaction times and their use of small refuges in the moss vegetation.

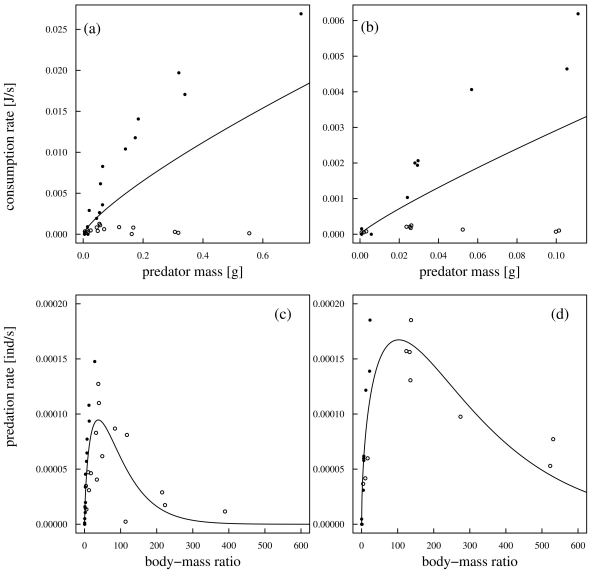

Figure 2.1.2: Laboratory measurements at the level of feeding links: per link consumption rates [J s^{-1}] depending on predator body mass (g), **(a)** beetles; **(b)** spiders and predation rates (ind s^{-1}) depending on predator–prey body mass ratios, **(c)** beetles; **(d)** spiders. Fitted model parameters (± SE): metabolic model (equation 3) for **(a)** beetles (b = 0.78 ± 0.22; K_0 = 0.02 ± 0.01; r^2 = 0.39; n = 32); **(b)** spiders (b = 0.87 ± 0.42; K_0 = 0.02 ± 0.02; r^2 = 0.36; n = 20); foraging model (equation 4) for **(c)** beetles (P_{max} = 9.46 10^{-5} ± 9.59 10^{-6}; R_{max} = 38.1 ± 6.17; α = 0.68 ± 0.16; r^2 = 0.6; n = 32); **(d)** spiders (P_{max} = 1.67 10^{-4} ± 1.45 10^{-5}; R_{max} = 103.1 ± 14.47; α = 0.54 ± 0·1; r^2 = 0.78; n = 20). Symbols indicate large prey (closed circles) and small prey (open circles).

Macroecological energy fluxes

Synthesizing macroecological abundance–mass relationships with the metabolic model (Eqn. 2.1.6a) and the foraging model (Eqn. 2.1.6b) yields predictions on per capita energy fluxes from a prey population to a predator individual with respect to predator and prey mass (Fig. 2.1.3a,b). Due to assumed constants (see Fig. 2.1.3 legend) the predicted fluxes should be interpreted only qualitatively. The predictions are based on the measured laboratory per link consumption and predation rates for beetles (Fig. 2.1.2a,c), but calculations based on the results for spiders yield qualitatively identical predictions (results not shown). The metabolic model predicts a continuous increase in per capita energy fluxes with increasing predator mass and decreasing prey mass (Fig. 2.1.3a). In contrast, the foraging model predicts a hump-shaped relationship between per capita energy fluxes and predator masses, where the hump increases with prey mass (Fig. 2.1.3b).

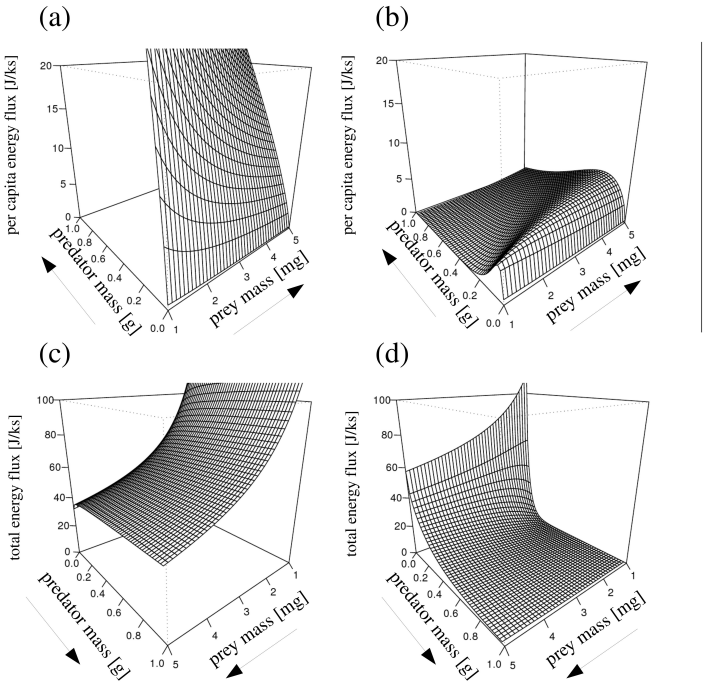

Figure 2.1.3: Per capita (**a,b**: from a prey population to a predator individual) and total (**c,d**: from a prey population to a predator population) energy flux as predicted by the synthetic models combining macroecological abundance–mass relationships with the metabolic model: **(a)** equation 2.1.6a; **(c)** equation 2.1.7a; or the foraging model: **(b)** equation 2.1.6b; **(d)** equation 2.1.7b, depending on predator **(g)** and prey body mass (mg). Calculations are based on per link consumption rates (**a,c**, see Fig. 2.1.2a) or predation rates (**b,d**, see Fig. 2.1.2c) and assumed constants: $E'_0 = E_0 = N_0 = 1$; $N'_0 = 30$; $\varepsilon = 7$; $c = 0{\cdot}75$. Thus energy flux values should be interpreted only qualitatively. ks = 10^3 s.

Multiplying per capita energy fluxes (Fig. 2.1.3a,b) with predator abundances yields total energy fluxes between prey and predator populations. The metabolic model (Eqn. 2.1.7a) predicts that the total energy fluxes increase with increasing predator mass and decreasing prey mass (Fig. 2.1.3c). The highest fluxes should thus occur between the smallest prey and the largest predators. In contrast, the foraging model (Eqn. 2.1.7b) predicts that the highest fluxes should occur between the smallest predators and the smallest prey species (Fig. 2.1.3d).

f) Discussion

At the species level, we found a three-quarter power-law scaling of the metabolic rates with body masses for beetles, which corroborates metabolic theory (Brown et al. 2004). Consistent with prior findings (Foelix 1996), the respiration rates of spiders were lower than those of beetles. Surprisingly, however, we found a much weaker increase in spider metabolism with body mass than predicted by the metabolic theory. Potential explanations for this discrepancy include that (1) the relative contribution of metabolically active tissue to total body mass of small spiders might exceed that in large spiders due to different rates of excretion-storage in their skins (Foelix 1996); and (2) spider metabolism might be limited by factors other than the efficiency of their physiological transport networks (Meer 2006). Corroborating metabolic theory, our data illustrate that the per capita consumption rates of both predator groups follow a power-law increase with body mass and exceed the metabolic loss, thus enabling the persistence of the predators.

While each predator's metabolic rate and total consumption were well predicted by power-law functions of predator body mass, the energy fluxes along individual predator–prey links were not. When predator–prey body mass ratios exceeded a threshold (R_{max}), the energy fluxes were limited by a decreasing success rate of the predator attacks due to a higher escape efficiency of the prey. Without the constraints posed by limited attack success, the metabolic model predicts a much stronger increase in energy flux with prey abundance. Interestingly, the two predator groups in our study represent profoundly different feeding strategies: spiders are mainly day-active, optically oriented predators, whereas beetles are mainly nocturnal, tactile and olfactory predators. However, the hump-shaped relationship between predation rates and body mass ratios found for both predator groups was well predicted by a foraging model, which is consistent with prior studies in aquatic ecosystems (Aljetlawi et al. 2004; Byström et al. 2003; Finstad et al. 2006; Wahlström, Persson, Diehl, and Byström 2000). While these studies addressed predation rates in size-structured predator–prey interactions with respect to the body masses of individuals, we studied predation rates as a function of the average masses of predator and prey populations. The foraging model used here and in related studies (Aljetlawi et al. 2004; Wahlström, Persson, Diehl, and Byström 2000) is phenomenological, and the hump-shaped relationship is fit equally well by two power-laws ($P_{ij} \approx R^{\varphi}$ if $R \leq R_{max}$; $P_{ij} \approx R^{-\eta}$ if $R > R_{max}$). However, independent of the choice of model, the broad generality of this hump-shaped relationship across ecosystem types and predator groups suggests that metabolic energy-flux models (Emmerson and Raffaelli 2004; Peters 1983; Reuman and Cohen 2005) that do not account for this relationship may seriously overestimate per capita energy fluxes between large predators and small prey. Moreover, the hump-shaped relationship between predation rates and predator-prey body mass ratios contrasts classic population dynamic models using power-law per link consumption rates (Yodzis and Innes

1992), whereas it corroborates recent approaches with unimodal predation rates (Loeuille and Loreau 2005; Weitz and Levin 2006). These patterns suggest that, all else being equal, the dynamic coupling between large predators and small prey may generally be weaker than predicted by a simple metabolic model. As general principles that govern energy flux may be more tractable than those that determine the population dynamics of species interaction strengths, it is critical to explore more thoroughly how and when consumer foraging patterns can predict the dynamic consequences of a change in consumer abundance (Schmitz 2007).

Some caveats should be mentioned. First, all laboratory experiments were carried out with simple predator–prey pairs, not accounting for potentially more complex feeding behaviour of predators when multiple prey species or multiple predator individuals coexist (e.g. prey switching or interference competition). Second, our estimates of field energy fluxes assume that consumption rates increase linearly with prey abundances (encounter rates) (Emmerson and Raffaelli 2004; Neutel et al. 2002). Where handling and satiation lead to consumption saturation at high prey densities, we anticipate that energy fluxes should always saturate, rather than increase monotonically as prey body mass decreases (and thus prey abundance increases). Third, encounter rates may be influenced by body mass-related species traits such as the search area of the predator and the movement velocity of predator and prey (Aljetlawi et al. 2004). While these caveats may change some quantitative aspects of the model predictions (e.g. the continuous increase in total energy flux with decreasing prey body mass), qualitative differences among predictions of the metabolic and foraging models should be robust. Most importantly, this includes (1) the power-law (metabolic model) vs. hump-shaped (foraging model) relationship between per capita energy flux and predator body mass; and (2) the increase (metabolic model) vs. decrease (foraging model) in total energy flux with predator body mass. Future extensions of our approach will address how more complex foraging models that account for the caveats listed above may change the quantitative predictions of the models.

While metabolic theory accurately predicts physiological processes at the level of individuals (per capita metabolic demand and consumption) (Brown et al. 2004), it failed to accurately predict per link energy fluxes at high predator–prey body mass ratios. At these high ratios, energy fluxes were not driven by the predators' metabolic demand as assumed by metabolic theory. Instead, they depended primarily on behavioural aspects of the interaction, such as the prey's escape efficiency that increased with predator-prey body mass ratios (for $R > R_{max}$). Rooted in behavioural models of foraging theory, the hump-shaped foraging model successfully predicted the energy fluxes in the present study. Thus reconciling these two bodies of theory that successfully predict patterns at the level of individuals (metabolic theory) and links (foraging theory) will be an important step towards quantitative community ecology that predicts energy fluxes and abundances.

Interestingly, the predator–prey body mass ratios that characterize the maximum predation rates in our experiments are consistent with the average predator–prey body mass ratios found in natural food webs (Brose, Jonsson, et al. 2006). Consistent with prior studies (Aljetlawi et al. 2004; Byström et al. 2003; Finstad et al. 2006; Wahlström, Persson, Diehl, and Byström 2000; Wilson 1975) our results suggest that predators may efficiently exploit prey that fall within a specific size range. Such a contiguous feeding range is also consistent with successful theoretical concepts of adaptive (Uchida et al. 2007) and static food web topology (Loeuille and Loreau 2005; Stouffer et al. 2006; Williams and Martinez 2000). Moreover, the foraging model predicts energy fluxes through individual feeding links, which offers a new perspective on the distribution of interaction strengths within food webs that ultimately drive network stability (Brose, Williams, et al. 2006; Emmerson and Raffaelli 2004; Neutel et al. 2007).Specifically, our results suggest that the dominant per capita energy fluxes within a food web that are critically important for its stability (Bascompte and Melian 2005; Neutel et al. 2007; Otto et al. 2007) occur between predator–prey pairs of intermediate body mass ratios (Fig. 3b). If our results generalize to other predator groups and ecosystem types, this approach allows predicting quantitative energy fluxes in natural food webs (Bersier et al. 2002). Ultimately, we anticipate that this will enable a quantitative understanding of interaction strengths, energy fluxes and the stability of complex natural food webs.

2.2. Allometric functional response model: body masses constrain interaction strengths

a) Summary

1. Functional responses quantify the per capita consumption rates of predators depending on prey density. The parameters of these nonlinear interaction strength models were recently used as successful proxies for predicting population dynamics, food-web topology and stability.

2. This study addressed systematic effects of predator and prey body masses on the functional response parameters handling time, instantaneous search coefficient (attack coefficient) and a scaling exponent converting type II into type III functional responses. To fully explore the possible combinations of predator and prey body masses, we studied the functional responses of 13 predator species (ground beetles and wolf spiders) on one small and one large prey resulting in 26 functional responses.

3. We found (i) a power-law decrease of handling time with predator mass with an exponent of -0.94; (ii) an increase of handling time with prey mass (power-law with an exponent of 0.83, but only three prey sizes were included); (iii) a hump-shaped relationship between instantaneous search coefficients and predator–prey body-mass ratios; and (iv) low scaling exponents for low predator–prey body mass ratios in contrast to high scaling exponents for high predator–prey body-mass ratios.

4. These scaling relationships suggest that nonlinear interaction strengths can be predicted by knowledge of predator and prey body masses. Our results imply that predators of intermediate size impose stronger per capita top-down interaction strengths on a prey than smaller or larger predators. Moreover, the stability of population and food-web dynamics should increase with increasing body-mass ratios in consequence of increases in the scaling exponents.

5. Integrating these scaling relationships into population models will allow predicting energy fluxes, food-web structures and the distribution of interaction strengths across food web links based on knowledge of the species' body masses.

b) Introduction

Understanding constraints on species' interaction strengths is critically important for predicting population dynamics, food-web stability and ecosystem functions such as

biological control (Berlow et al. 2004; Montoya et al. 2006; Wootton and Emmerson 2005). Empirical and theoretical evidence suggests that predator and prey body masses are among the most important of these constraints (Berlow et al. 2008, 2009; Emmerson and Raffaelli 2004; Wootton and Emmerson 2005). Conceptually, these nonlinear interaction strengths are described by the magnitude and shape of functional responses that quantify per capita consumption rates of predators depending on prey abundance. One generalized functional response model is based on Holling's disk equation (Holling 1959a):

$$F_{(N)} = \frac{bN^{q+1}}{1 + bT_h N^{q+1}} \qquad (2.2.1)$$

where F is the per capita consumption rate, N is prey abundance, T_h is the handling time needed to kill, ingest and digest a resource individual, b is a search coefficient that describes the increase in the instantaneous search rate, a, with resource abundance, N:

$$a = bN^{q} \qquad (2.2.2)$$

where q is a scaling exponent that converts type II into type III functional responses (Rall et al. 2008; Williams and Martinez 2004). The hill exponent, h, used in some prior studies (Real 1977) is equivalent to q ($h = q + 1$).

Functional responses can be linear (type I, $T_h = 0$, increase up to a threshold abundance), hyperbolic (type II, $T_h > 0$, $q = 0$) or sigmoid (type III, $T_h > 0$, $q > 0$). While many early studies focused on type I and type II functional responses and ignored the scaling exponent, type III functional responses with scaling exponents larger than zero could occur more frequently than previously anticipated (Sarnelle and Wilson 2008). Under hyperbolic type II functional responses predation risks for prey individuals decrease with prey abundance causing inverse density-dependent prey mortality, which can lead to unstable boom-burst population dynamics (Hassell 1978; Oaten and Murdoch 1975). In contrast, increasing predation risks under sigmoid functional responses can yield an effective per capita top-down control that often prevents such unstable dynamics (Gentleman and Neuheimer 2008; Rall et al. 2008). Slight differences in functional response parameters can thus have drastic consequences for population and food-web stability in natural ecosystems (Brose, Williams, et al. 2006; Fussmann and Blasius 2005; Oaten and Murdoch 1975; Rall et al. 2008; Williams and Martinez 2004).

Allometric scaling theories provide a conceptual framework how body masses could determine foraging interactions (Peters 1983; Brown et al. 2004). The maximum consumption rates realized at infinite prey densities are proportional to the inverse of handling time and independent of the success of the attacks (Koen-Alonso 2007; Yodzis and Innes 1992). Consequently, the 3/4 power-law scaling of maximum consumption with predator body mass

(Carbone et al. 1999; Peters 1983) suggests that handling time should follow a negative ¾ power-law with predator body mass. This trend is qualitatively supported, though studies reported linear (Hassell et al. 1976; Spitze 1985), power-law or exponential relationships (Aljetlawi et al. 2004; Hassell et al. 1976; Jeschke and Tollrian 2005b; Thompson 1975).

The characteristic components of search rates include the reactive distance between predator and prey (i.e. the distance between predator and prey individuals at which a predator individual responds to the presence of the prey) and the capture success. While the reactive distance increases with the body masses of the predators (i.e. large predators have a larger visual range than small predators), the capture success decreases with predator mass above an optimum body mass ratio (Aljetlawi et al. 2004; Brose et al. 2008). A further explanation for the low capture success is that the predator's motivation to capture small prey of limited energy content is low (Petchey et al. 2008). Together, these patterns in reactive distances and capture success may explain the hump-shaped relationships between search rates and predator-prey body-mass ratios with a maximum search rate at intermediate (optimum) body-mass ratios documented in prior studies (Aljetlawi et al. 2004; Brose et al. 2008; Hassell et al. 1976; Vonesh and Bolker 2005; Wahlström, Persson, Diehl, and Byström 2000). However, these studies were either restricted to search rates of single predator–prey interactions (with variance in individual size) or studied multiple predator-prey search rates at a single, constant prey density. Thus, none of these prior studies has addressed body-size constraints on functional responses across species.

In this study, we quantified systematic effects of predator and prey masses on functional response parameters (handling time, search coefficient and scaling exponent) across different predator–prey interactions. While more complex functional response models accounting for digesting time and interference behaviour exist (Jeschke et al. 2002; Kratina et al. 2009; Schenk et al. 2005; Skalski and Gilliam 2001), testing for their body-size dependence was left for subsequent studies. Instead, the allometric functional response model addressed here provide an empirical basis for an understanding of body-size constraints on interaction strengths, food-web topology (Petchey et al. 2008) and dynamics (Brose et al. 2008; Brose, Williams, et al. 2006; Otto et al. 2007; Rall et al. 2008).

c) Methods

The predators of our experiment were carabid beetles (*Abax parallelepipedus*, *Carabus nemoralis*, *Pterostichus melanarius*, *Pterostichus oblongopunctatus*, *Harpalus rufipes*, *Calathus fuscipes*, *Calathus melanocephalus*, *Anchomenus dorsalis* and *Poecilus versicolor*; Carabidae: Coleoptera) and wolf spiders (*Trochosa terricola*, *Pardosa lugubris*; Aranea: Lycosidae) sampled in pitfall traps. The juvenile weight classes of 1, 3 and 10 mg of Trochosa

were considered as trophic species as they vary in consumption rates and preferences for the different prey species (Brose et al. 2008; Rickers 2005). We used *Alphitobius diaperinus* larvae (Coleptera; Tenebrionidae; hereafter: *Alphitobius*), flightless adults of *Drosophila hydei* (Diptera; Drosophilidae, hereafter: *Drosophila*) and *Heteromurus nitidus* (Collembola; Entomobryidae, hereafter: *Heteromurus*) as prey.

Functional Response Experiments

To explore fully possible combinations in predator and prey body masses, we studied the functional response of each predator on one small and one large prey. For the beetles, we used flightless *Drosophila* as small prey and *Alphitobius* as large prey. For the spiders, we used *Heteromurus* as small prey and flightless Drosophila as large prey. Each experimental unit included one predator individual and prey at different initial densities that were varied between low densities (1, 3, 5, 10, 20, 30 prey individuals per experimental arena) and higher prey densities that were adjusted to each specific predator–prey combination to reach saturation in the predators per capita consumption rate (e.g. 120 individuals of *Drosophila* for the small predator *Anchomenus dorsalis* and 4000 individuals of *Drosophila* for the large predator *Carabus nemoralis*). Six replicates per prey density were established. The predator individuals were kept separate in plastic jars dispersed with water and were deprived of food for 1 week prior to the start of the experiments. The experiments were performed in Perspex® (Degussa AG, Darmstadt, Germany) arenas (20 x 20 x 10 cm) covered with lids that had holes to allow gas exchange. The ground was covered with moist plaster (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.43 g dry weight) that was first dried for several days at 40°C to exclude other animals and then re-moisturised. The experiment was run for 24 h with a day / night rhythm of 12 / 12 h dark / light and temperature of 15°C. Initial and final prey densities were used to calculate the number of prey eaten. Control experiments without predators showed that prey mortality or escape did not influence our experiments. The predators were weighed before and after the experiment to calculate the mean body mass of each predator and the body-mass ratio of each predator-prey pair (Table 2.2.1).

Statistical Analyses

In the present study, the prey densities changed during the experimental period with each consumption event. To account for this prey depletion during the experiments, we used a generalized model of Rogers's random predator equation (Juliano et al. 2001; Rogers 1972):

$$N_e = N_0(1-\exp(bN_0^q(T_h N_e - T))) \quad (2.2.3),$$

where N_e is the number of prey eaten, N_0 is the initial prey density, b is the search coefficient

(search rate $a = bN_0^q$), Th is the handling time, T is the experimental duration time and q is the scaling exponent. We fitted equation (2.2.3) to the experimental data using Newton's method in **SAS** 9.1 (Juliano et al. 2001) to obtain parameter estimates. We prevented (i) negative scaling exponents (i.e. decreases in search rates with prey density) and (ii) negative handling times. Subsequently, we tested for effects of predator and prey masses on handling times, search coefficients and hill exponents. We used linear least-squares regressions to test for relationships between $\log_{10}$ handling time vs. $\log_{10}$ predator mass and $\log_{10}$ prey mass:

$$\log_{10} T_h = p \log_{10} M_P + n \log_{10} M_N + \log_{10} T_{h(0)} \qquad (2.2.4)$$

with T_h as handling time, M_P as predator mass, M_N as prey mass, and p, n, $T_{h(0)}$ as constants. Hump-shaped relationships between $\log_{10}$-transformed search-coefficients, b, and predator–prey body-mass ratios, R, were tested by fitting the following size–search-coefficient curve in **R** (R-Project 2.8.1, free statistic software; The R Foundation for Statistical Computing, Vienna, Austria):

$$\log_{10}(b_{(R)}+1) = A \frac{\exp(\varepsilon(\Phi - \log_{10}(R+1)))}{1+\exp(\beta\varepsilon(\Phi - \log_{10}(R+1)))} \qquad (2.2.5)$$

where A is a constant, Φ represents the body mass ratio at which 50% of the maximum search coefficient is reached, e is the rate of change in search with size controlling the steepness of the curve, R is the body-mass ratio and b determines the asymmetry of the curve (Vonesh and Bolker 2005). To find the optimum body mass ratio, R_0, where the maximum search coefficient is reached, the first derivative of equation (2.2.4) has to be set equal to zero and solved for R_0, resulting in the following equation (Vonesh and Bolker 2005):

$$\log_{10}(R_0+1) = \frac{\Phi + \log_{10}(\beta - 1)}{\varepsilon\beta} \qquad (2.2.6)$$

The solution of equation (2.2.6) can be inserted in equation (2.2.5) to calculate the maximum search coefficient, $b_{max}(R_0)$.We tested for significant differences in scaling exponents, q, between predator-prey pairs using an ANOVA. Subsequently, we employed two contrast analyses (one for spiders and one for beetles) to test our hypothesis that the scaling exponent is higher for high predator-prey body-mass ratios (small prey) than for low ratios (large prey).

d) Results

Across the 26 functional responses of the present study (Table 2.2.1), we found substantial variance in search coefficients [$4.86 \leq b \leq 4.07 \times 10^3$ (cm^2 day^{-1} ind^{-q} $Arena^q$)], handling times [$10^{-3} \leq T_h \leq 9.45 \cdot 10^{-1}$ (day $ind.^{-1}$)], and scaling exponents ($0 \leq q \leq 1.42$). In subsequent analyses, we related this variance in functional response parameters to predator–prey body-

mass ratios spanning roughly three orders of magnitude from 0.65 to 532 (Table 2.2.1).

Table 2.2.1: Mean predator and prey weights, predator–prey body-mass-ratios, and functional response parameters: N = number of replicates, b = search coefficient ($cm^2\ day^{-1}\ ind^{-q}\ Arena^q$), T_h = handling time (day ind.)1), SE = standard error, q = scaling exponent, weight = mean predator weight (mg) and R = predator–prey body-mass ratio

	N	b	SE	T_h	SE	q	SE	Weight	R
Beetles with large prey *Alphitobius diaperinus* [23.26 mg]									
Anchomenus dorsalis	3	0	0	0	0	0	0	14.50	0.65
Calathus melanocephalus	3	0	0	0	0	0	0	17.54	0.79
Calathus fuscipes	36	$9.33*10^{2}$	$1.39*10^{-3}$	0.52	0.07	0	0.0	71.52	3.08
Pterostichus oblongopunctatus	30	$3.88*10^{3}$	$1.27*10^{-2}$	0.62	0.06	0	0.0	69.65	2.99
Harpalus rufipes	48	$1.76*10^{3}$	$3.73*10^{-3}$	0.41	0.06	0	0.0	129.10	5.55
Pterostichus melanarius	36	$4.07*10^{3}$	$7.83*10^{-3}$	0.25	0.02	0	0.0	158.02	6.79
Abax parallelepipedus	24	$1.49*10^{3}$	$1.01*10^{-3}$	0.10	0.01	0	0.0	302.00	12.98
Carabus nemoralis	42	$2.98*10^{2}$	$8.62*10^{-4}$	0.06	0.02	0.11	0.7	513.14	22.06
Beetles with small prey Drosophila hydei [1.42 mg]									
Anchomenus dorsalis	57	$3.63*10^{1}$	$1.48*10^{-4}$	0.21	0.03	0.86	1.1	14.49	10.21
Calathus melanocephalus	57	$8.52*10^{1}$	$2.99*10^{-4}$	0.20	0.02	0.68	1	17.54	12.35
Calathus fuscipes	46	4.86	$2.00*10^{-5}$	0.10	0.01	1.42	0.8	81.82	57.62
Pterostichus oblongopunctatus	45	$2.53*10^{1}$	$7.60*10^{-5}$	0.12	0.01	1.08	0.7	65.05	45.81
Harpalus rufipes	54	$1.49*10^{2}$	$3.03*10^{-4}$	0.06	0.01	0.54	0.5	41.85	29.47
Pterostichus melanarius	54	$4.78*10^{1}$	$1.44*10^{-4}$	0.04	0.01	0.53	0.5	148.03	104.3
Abax parallelepipedus	90	$5.07*10^{1}$	$3.27*10^{-7}$	0.02	$2*10^{-3}$	1.41	0.7	287.58	202.5
Carabus nemoralis	76	$3.32*10^{1}$	$3.01*10^{-7}$	$5*10^{-3}$	0.01	0.68	0.7	463.84	326.7
Spiders with large prey Drosophila hydei [1.42 mg]									
Pardosa lugubris	54	$1.50*10^{3}$	$8.25*10^{-3}$	0.14	0.02	0.26	1.9	29.37	20.68
Trochosa terricola, 3 mg	42	$1.22*10^{3}$	$1.64*10^{-3}$	0.94	0.09	0	0	3.45	2.42
Trochosa terricola, 10 mg	36	$1.90*10^{3}$	$4.72*10^{-3}$	0.47	0.06	0	0	11.41	8.03
Trochosa terricola, adult	70	$2.07*10^{2}$	$4.71*10^{-4}$	0.03	$4*10^{-3}$	0.40	0.4	84.81	59.72
Spiders with small Heteromorus nitidus [0.15 mg]									
Pardosa lugubris	60	$1.27*10^{1}$	$3.90*10^{-5}$	0.05	0.01	1.10	0.6	25.77	171.8
Trochosa terricola, 3 mg	48	$3.43*10^{2}$	$6.76*10^{-4}$	0.10	0.01	0.5	0.7	3.08	20.51
Trochosa terricola, 10 mg	60	$1.27*10^{2}$	$3.25*10^{-4}$	0.02	0.01	0.40	0.5	10.61	70.75
Trochosa terricola, adult	88	$7.66*10^{1}$	$1.73*10^{-4}$	0.01	$1*10^{-3}$	0.10	0.3	79.79	532,4

The handling time exhibited a power-law decrease with increasing predator mass with an exponent of -0.94 ± 0.09 (mean ± SE, Fig. 2.2.1a) and a power-law increase with prey mass with an exponent of 0.83 ± 0.07. We caution, however, that these analyses are based on only three prey size classes and the latter exponent illustrates the relationship only qualitatively. Together, predator and prey mass explained 89% of the variation in handling time. The search coefficient followed a hump-shaped relationship with predator-prey body-mass ratios (Fig.

2.2.1b, r^2 = 0.74). The hump-shaped nature of this relationship depends on two data points with $\log_{10}$ mass ratios smaller than 0.5 (Fig 2.2.2b), but other predator species in this body-mass range have not been available. The maximum search coefficient, b_{max} = 2161.5, was reached at intermediate body-mass ratios of R_0 = 3.15 (i.e. predators are roughly three times larger than their prey). As handling time is proportional to the inverse of the predators' maximum consumption rates, the maximum nonlinear interaction strengths increase with the body-mass ratios (Fig 2.2.2). These maximum nonlinear interaction strengths are realized at the highest prey densities. At lower prey densities, the nonlinear interaction strengths also depend on successful search rates, which causes hump-shaped relationships with body-mass ratios (Fig. 2.2.2). The scaling exponent, q, was significantly higher for beetles and small prey (q = 0.89 ± 0.15, mean ± SE) than for beetles with large prey (q = 0.02 ± 0.11, Fig. 2.2.1c). This indicates that the nonlinear interaction strengths between beetles and their prey were best described by type III functional responses for high predator–prey body-mass ratios when beetles fed on small prey (Fig. 2.2.2c), whereas type II functional responses characterized their interactions under low predator-prey body-mass ratios with large prey (Fig. 2.2.2a). While a similar pattern of type-III functional responses with small prey (high body-mass ratios; q = 0.52 ± 0.16, mean ± SE) and type-II functional responses with large prey (low body-mass ratios; q = 0.17 ± 0.23, mean ± SE) was found for spiders (Fig. 2.2.2d, b), this difference in the scaling exponent was not statistically significant (Fig. 2.2.1c, contrast analysis for spiders: P = 0.17).

e) Discussion

We studied the influence of predator and prey body masses on 26 functional responses of common terrestrial arthropod predators. We found: (i) power-law scaling in handling times with predator and prey masses, (ii) hump-shaped relationships between search coefficients and predator-prey body-mass ratios, and (iii) increases in the scaling exponent with body-mass ratios (only significant for beetles). Our findings provide evidence of how functional response parameters vary across predator-prey interactions of different body-mass ratios. We focused on two groups of generalist predators with different feeding

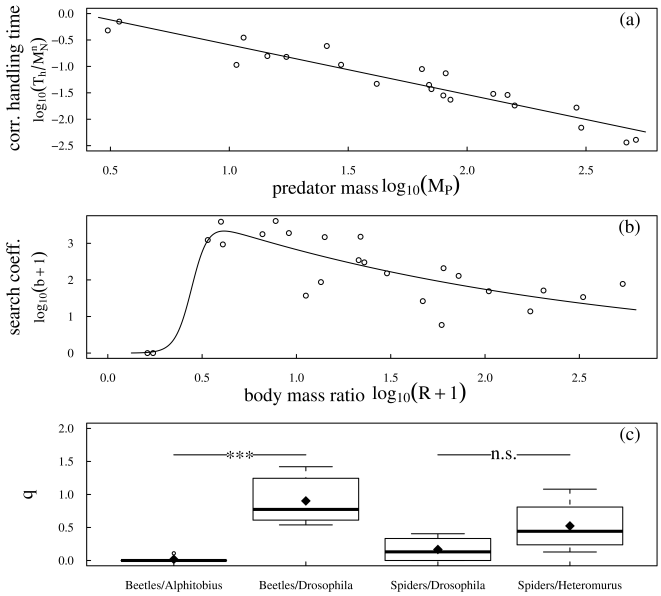

Figure 2.2.1: Allometric scaling of functional response parameters: **(a)** $\log_{10}$ handling time (min ind.$^{-1}$) decreases with $\log_{10}$ predator mass (mg); eqn (4): p = -0.94 ± 0.09 (mean ± SE, $P < 0.001$), n = 0.83 ± 0.07 ($P < 0.001$), $T_{h(0)}$ = 0.35 ± 0.14 ($P <$ 0.01), r^2 = 0.887; note that handling time was normalized by the prey body-mass term in Eqn. (2.2.4): corr$T_h = \log_{10} T_h$) $n\log_{10} M_N$; **(b)** search coefficients (cm^2 day^{-1} ind^{-q} Arena^q) follow a hump-shaped relationship with predator–prey body-mass ratios; eqn (5): A = 3.69 ± 0.52 ($P < 0.001$), ε = 0.48 ± 0.11 (P < 0.001), F = 0.45 ± 0.154 (P < 0.01) and b = 47.13 ± 88.67 (n s.), r^2 = 0.74; **(c)** scaling exponents, q, and predator–prey

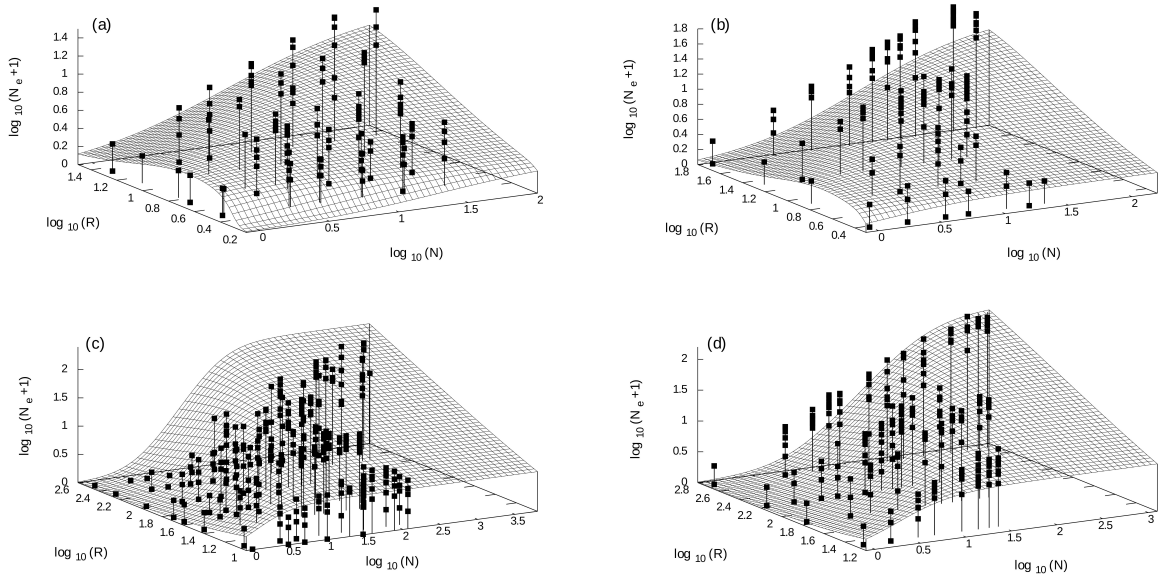

Figure 2.2.2: Experimental per capita consumption rates (N_e) depending on predator–prey body-mass ratios (R) and prey density (N) with allometric functional responses according to the allometric scaling functions of Fig. 2.2.1 for **(a)** Beetles/Alphitobius (low predator–prey body-mass ratios), **(b)** Spiders/Drosophila (low ratios), **(c)** Beetles/Drosophila (high ratios), **(d)** Spiders/Heteromurus (high ratios).

strategies: beetles are mainly nocturnal, tactile and olfactory, whereas spiders are day active and optically oriented. The similarity in our findings for both predator groups suggests the broad generality of our results.

Interestingly, we found an exponent of -0.94 (SE = ±0.09) in the relationship between handling time and predator body mass, which is significantly different from the exponent of -0.75 initially predicted based on metabolic theory (Brown et al. 2004; Carbone et al. 1999; Peters 1983; Yodzis and Innes 1992). Thus, larger predators had lower handling times and smaller predators had higher handling times than expected based on metabolically driven processes. Assuming that metabolism mainly drives the digestive part of handling, it follows that the speed of morphologically constrained handling processes such as killing and ingesting the prey increases more steeply with predator mass than metabolic processes. For instance, if gut and stomach size are proportional to body size the maximum ingestion will also be proportional to body size. Consequently handling time should be inversely proportional to body size, which is consistent with our results. Consistent with most other functional response experiments, the short 24-h time period of our experiments thus emphasizes morphological over digestive constraints on handling times. An improved mechanistic understanding of the scaling exponents thus requires differentiating between ingesting and digesting times in studies with varying experimental duration (Jeschke et al. 2002). While metabolic arguments suggest power-law scaling of digesting times with predator masses, ingesting times could be inversely proportional to body mass.

Instead of the expected linear increase in handling time with prey mass (exponent of unity), we found a scaling exponent of 0.83 ± 0.07 (mean ± SE). One plausible but speculative explanation for this difference could be that the energy content of the prey does not increase proportional to the prey mass. In this case, larger prey would contain more indigestible body parts (e.g. exoskeleton) that impose limitations on ingesting or digesting the prey body. However, a detailed analysis of the morphological and energetic structure of the prey biomass was beyond the scope of the present study. Moreover, we caution that our results were based on only two prey types for each of the predator groups, which may confound the prey-mass scaling relationships presented here. While our study demonstrates that handling time-scales with prey mass, subsequent studies should include a broader variation in prey body masses to more specifically address the exact exponent of this scaling relationship.

Consistent with prior studies investigating search coefficients at constant prey densities (Brose et al. 2008; Wahlström, Persson, Diehl, and Byström 2000), our results corroborate the hump-shaped relationship between search coefficients and predator-prey body-mass ratios (Figs 2.2.1b and 2.2.2). While the present study was lacking data of direct behavioural observations, we follow prior studies in suggesting that the following behavioural constraints could be responsible for this hump-shaped relationship. Small predators (with low predator-

prey body-mass ratios) have a small search area, and they have difficulties in subduing prey larger than themselves leading to inefficient attacks. Large predators (with high predator-prey body-mass ratios) have difficulties in catching small prey individuals, since the much smaller prey have faster reaction times and high escape efficiencies (Brose et al. 2008). At intermediate predator-prey body-mass ratios, however, the highest search coefficients were found, because predators are less restricted in subduing or catching the prey individuals. While the hump-shaped scaling of search coefficients with predator-prey body-mass ratios is supported by our data, these behavioural constraints remain hypotheses to be tested.

In our study, the two different predator groups were most efficient at a predator-prey body-mass ratio of $R_0 = 3.15$ (i.e. when predators were roughly three times larger than their prey). In a prior study, however, the group-specific capture mechanism of predators (e.g. sit-and-move vs. chasing predators) was shown to have a large effect on the optimum predator-prey body mass ratio (Troost et al. 2008) suggesting that the optimum body-mass ratio documented here for epigeic spiders and beetles should not necessarily apply to other predator groups. Interestingly, in other ecosystems, a negative relationship between prey density and search rates could occur if the prey employs group defence mechanisms such as swarming (e.g. mammals or fish) (Jeschke and Tollrian 2005a). With respect to defence mechanisms of prey, the prey type may thus also influence these scaling relationships.

Moreover, prior studies reported maximum search coefficients of differently sized perch at $R_0 = 49.8$ for planktonic prey of 0.5 mm and at $R_0 = 78.9$ for prey of 1 mm size (Wahlström, Persson, Diehl, and Byström 2000), and $R_0 = 103.1$ for wolf spiders and $R_0 = 83.1$ for ground beetles in terrestrial ecosystems (Brose et al. 2008). These studies were based on the simplifying assumption of constant prey densities, whereas the present study overcame this assumption by varying prey densities to estimate search rates of functional responses. While our results support the predicted hump-shaped search rates under varying prey densities, they also demonstrate that optima in the search coefficients were realized at body-mass ratios of $R_0 = 3.15$, which is approximately one order of magnitude lower than the optimum body-mass ratios of a prior study with the same species (R_0 of 83.1 or 103.1; Brose et al. 2008). This difference suggests that studies at constant prey densities might yield inaccurate estimates of optimum body-mass ratios. Interestingly, the optimum body-mass ratio of the present study is highly consistent with the geometric average body-mass ratio of 3.98 between invertebrate predators and their prey found in terrestrial food webs (Brose, Jonsson, et al. 2006). This implies that many interactions in terrestrial communities might be realized with maximum instantaneous search rates.

Consistent with prior studies, our results suggest that predators efficiently exploit prey within a specific size range. While our present results suggest that terrestrial predators are less specialized than previously anticipated (Brose et al. 2008), striking differences in optimum

body-mass ratios, R_0, between these studies are evident. Disentangling whether these differences depend on the organisms investigated (e.g. beetles and spiders vs. fishes) or on ecosystem characteristics (terrestrial vs. pelagic) would require additional studies of varying predator groups in different ecosystem types. Eventually, these studies will allow addressing evolutionary and ecologically relevant questions of different optimum body-mass ratios and degrees of specialization across organism groups and ecosystem types.

In this study, we present evidence from systematic laboratory experiments that the scaling exponent, q, may increase with the predator-prey body-mass ratio, though this difference was only significant for ground beetles. This corroborates prior findings that type III functional responses could occur more frequently than previously anticipated (Sarnelle and Wilson 2008). Interestingly, a similar increase in the scaling exponent with prey size was reported based on gut content analysis of marine minke whales (Smout and Lindstroem 2007). Together, these results could indicate a potentially broad universality of increases in scaling exponents with predator-prey body-mass ratios across different ecosystems.

It has been stressed that functional response experiments should apply a realistic habitat structure in the experimental arenas to create more natural experimental settings, since prey density often also relates to habitat structure (Crawley 1992; Real 1977). Moreover, it was hypothesized that adding such habitat structure could lead to a change of the functional response type as a consequence of potential hiding refuges for the prey (Crawley 1992; Hassell et al. 1977; Real 1977). Accounting for this fact, our experimental design included a constant density of moss as a natural habitat structure. Certainly, it would be important to replicate the functional responses of the present study across different moss densities to address how the body-mass effects documented here interact with effects of habitat complexity. Thus, the scaling exponents and attack coefficients of the present study should be interpreted only qualitatively, because different levels of habitat complexity should affect the absolute values of these parameters.

As a general, qualitative pattern, we found that this moss provided refuges for small prey from predation by large predators (high body-mass ratios) resulting in sigmoid, type III functional responses with scaling exponents higher than zero. In contrast, predators of similar body mass as their prey (i.e. low body-mass ratios) were able to follow the prey into the hiding places within the habitat structure resulting in functional responses of type II with scaling exponents of zero. These observations during the experiments provide an explanation for the observed shift from functional responses of type II at low predator-prey body-mass ratios to functional responses of type III at high predator-prey body-mass ratios.

Interestingly, this suggests that population dynamics are stabilized by increasing body-mass ratios as a result of increasing scaling exponents (Brose, Williams, et al. 2006; Oaten and

Murdoch 1975; Rall et al. 2008; Williams and Martinez 2004). While previous studies documented that high body-mass ratios stabilize population and food-web dynamics via reductions in the per unit biomass rates of metabolism and consumption (Brose et al. 2008; Brose, Williams, et al. 2006; Emmerson and Raffaelli 2004), the increases in the scaling exponent documented here suggest an additional mechanism of how high body-mass ratios stabilize natural ecosystems.

We have presented the scaling of functional response parameters with predator and prey body masses with quantitative parameter estimates. This might be interpreted as an opportunity to estimate quantitatively functional responses based on body masses. However, we caution that this would be a misuse of our model: even in the case of the functional responses of the present study (Table 2.2.1) backward estimation of the per capita consumption rates based on the allometric functional response model yields substantial over- or under-estimations (Fig. 2.2.2). As other scaling models such as species-area relationships or metabolic scaling theory, the results presented here should be interpreted as a documentation of patterns across a body-mass scale. For instance, nobody would seriously estimate the species richness of Borneo based on a global species–area relationship, whereas this scaling model certainly has a tremendous value as conceptual cornerstone of biogeography. In the same vein, we suggest using the allometric functional response model presented here as an indication of scaling behaviour in foraging ecology. Integrating these scaling relationships into population models will allow predicting general trends in energy fluxes (Brose et al. 2008), food-web structures (Petchey et al. 2008), and the distribution of interaction strengths across food-web links (Bersier et al. 2002). Eventually, combining allometric functional response models with those of food-web structure (Cattin et al. 2004; Petchey et al. 2008; Williams and Martinez 2000) may allow a more detailed understanding how the distribution of body masses across species in natural ecosystems determines population and food-web stability (Brose, Williams, et al. 2006; Otto et al. 2007; Rall et al. 2008).

2.3. Temperature, predator-prey interaction strength and population stability

a) Abstract

Warming could strongly stabilise or destabilise populations and food-webs by changing the interaction strengths between predators and their prey. Predicting the consequences of warming requires understanding how temperature affects ingestion (energy gain) and metabolism (energy loss). Here, we studied the temperature dependence of metabolism and ingestion in laboratory experiments with terrestrial arthropods (beetles and spiders). From this data, we calculated ingestion efficiencies (ingestion / metabolism) and per capita interaction strengths in the short and long term. Additionally, we investigated if and how body mass changes these temperature dependencies.

For both predator groups, warming increased metabolic rates substantially, whereas temperature effects on ingestion rates were weak. Accordingly, the ingestion efficiency (the ratio of ingestion to metabolism) decreased in all treatments. This result has two possible consequences: on the one hand it suggests that warming of natural ecosystems could increase intrinsic population stability, meaning less fluctuations in population density; on the other hand, decreasing ingestion efficiencies may also lead to higher extinction risks due to starvation. Additionally, predicted long term per capita interaction strengths decreased with warming, which suggests an increase in perturbation stability of populations, i.e. a higher probability of returning to the same equilibrium density after a small perturbation. Together, these results suggest that warming has complex and potentially profound effects on predator-prey interactions and food-web stability.

b) Introduction

Understanding the impact of global warming on the stability of populations and critical ecosystem processes is one of the most important scientific challenges we currently face (Hughes 2000; Mann et al. 1998). Warming may affect a species by changing the strength of its interactions (e.g. competition or predator-prey interactions) with coexisting species. By modifying interaction strength warming may not only directly affect population densities, but it may also indirectly affect the population size of coexisting species (Berlow et al. 2009). Indirect effects occur when a species affects the *per capita* population growth rate of a non adjacent species within an ecological network such as a food web. These indirect effects among species can be more important than direct effects in driving the outcomes of

perturbations (Abrams 1995; Menge 1997; Yodzis 2000; Ives & Cardinale 2004). Moreover, the pattern and strength of species interactions determine the stability of populations and food webs (Brose 2008; Brose, Williams, et al. 2006; Emmerson and Yearsley 2004; May 1973; Neutel et al. 2002, 2007; Otto et al. 2007; de Ruiter et al. 1995). Thus, understanding how temperature affects interaction strengths is of vital importance for predicting consequences of global warming for the stability of populations, communities and ecosystem processes (Hughes 2000).

Two important aspects of population stability (McCann 2000) are (1) intrinsic stability expressed as the inverse of variability in population density over time (Brose, Williams, et al. 2006), inversely related to predator ingestion efficiencies (Rall et al. 2008; Vasseur and McCann 2005; Yodzis and Innes 1992), which are defined as the ratio of ingestion to metabolism; and (2), perturbation stability, quantifying the resistance of a population to a small perturbation measured as the probability of returning to the same equilibrium density (Emmerson and Raffaelli 2004). Perturbation stability decreases with increasing *per capita* interaction strength (hereafter: interaction strength) expressing the effects of a predator individual on the abundance of prey populations (May 1972; de Ruiter et al. 1995). Often, interaction strength is measured as the log ratio between prey density in treatments with predators versus prey density in treatments without predators (Berlow et al. 2004, 1999). The time scales used to calculate interaction strength varies between short term experiments of some days (Emmerson and Raffaelli 2004) or weeks (Sanford 1999) and longer experiments over several months (Berlow 1999). These differences in time scales may result in different outcomes and interpretations of experiments (Walther 2007). In particular, interaction strengths on a short time scale (days) depend primarily on predator ingestion rates while ignoring numerical responses in predator and prey abundances. However, on a long time scale (month, years), interaction strengths are also influenced by the the rates of prey growth and prey abundance (Berlow et al. 2009). Therefore, predicting the consequences of warming requires an understanding of temperature effects on the rates of ingestion and metabolism of the predators (with implications for short term interaction strengths) and the growth rates and abundances of the prey species (with additional implications for long term interaction strengths).

The Metabolic Theory of Ecology (MTE) offers a general framework for tackling these questions by suggesting: (i) three-quarter power-law increases in the rates of metabolism, ingestion and growth with organism body mass, (ii) a three-quarter power-law decrease in abundance with body mass within a single trophic level, and (iii) exponential scaling of these rates and abundance with temperature, where the strength of these scaling relationships is determined by an activation energy, E (Brown and Gillooly 2003; Brown et al. 2004; Gillooly et al. 2001; Meehan 2006a). Despite an intensive debate on the exact exponents, the power-law

(body mass) and the exponential (temperature) scaling of metabolism find broad empirical support (Brown et al. 2004; Clarke 2004; Kozlowski and Konarzewski 2004; Makarieva et al. 2005; Savage, Gillooly, Brown, et al. 2004).

In the case of ingestion, the scaling with body mass and temperature remains hotly debated (Brose et al. 2008; Brose; Brown et al. 2004; Carbone et al. 2007; Peters 1983; Vasseur and McCann 2005; Vucic-Pestic et al. 2010). In contrast to MTE predictions (Peters 1983), recent foraging studies have documented a hump-shaped relationship between ingestion rates and predator-prey body-mass ratios (Brose et al. 2008; Vonesh and Bolker 2005; Vucic-Pestic et al. 2010; Wahlström, Persson, Diehl, and Bystrom 2000). This implies that handling and digestion constrain predator ingestion rates at low predator-prey body-mass ratios (i.e. when prey species are relatively large), whereas catching efficiencies limit predator ingestion rates at high ratios (i.e. when prey species are relatively small). While some prior studies showed that ingestion increases with temperature (Kingsolver and Woods 1997; Thompson 1978) others concluded that ingestion is not effected by warming (Woodward and Hildrew 2002). Unfortunately, studies that include both, temperature-dependent ingestion and metabolism of predators, are scarce (Abrahams et al. 2007; Kingsolver and Woods 1997; Vasseur and McCann 2005), and it remains unknown whether the different processes leading to handling and catching limitation of large (left side of the hump-shaped relationship, (Brose et al. 2008) and small prey (right side of the hump-shaped relationship), are similarly influenced by temperature.

Here, we address these deficiencies by quantifying the temperature dependence of metabolism and ingestion (of small and large prey) of terrestrial arthropods (beetles and spiders) across a range of body masses. The predator and prey species of our experiments were chosen to reflect the predator-prey body-mass ratios of natural food webs (Brose et al. 2006a) and both sides of the hump-shaped relationship between ingestion and body-mass ratios documented in a prior study with the same species (Brose et al. 2008; Vucic-Pestic et al. 2010). All experiments were replicated at three environmental temperatures (8°C, 15°C and 22°C) representing the natural gradient of spring and summer temperatures in central Germany (Deutscher Wetterdienst 2007). Based on these experiments, we quantified how temperature affects ingestion efficiencies, short term and long term interaction strengths, which provides the information required to address the effect of temperature on both intrinsic and perturbation stability of populations and food webs.

c) Material and Methods

Respiration and ingestion experiments

We investigated how predator metabolism varied with temperature. Specifically, we measured the O_2 consumption of eight carabid beetle species (*Abax paralellepipedus*, *Carabus auratus*, *Harpalus affinis, Notiophilus biguttatus, Platynus dorsalis*, *Poecilus versicolor Pseudophonus rufipes and Pterostichus oblongopunctatus*) and six species of lycosid and pisaurid spiders (*Alopecosa cuneata*, *Pardosa lugubris, Pardosa palustris*, *Pirata latitans, Pirata piraticus* and *Pisaura mirabilis*). O_2 consumption of the beetles and spiders was measured in an automated electrolytic microrespirometer (Scheu 1992). We converted the individual O_2 consumption [ml/s] into energetic equivalents of metabolism I_j [J/s] by assuming that 1 ml O_2 equals 20.1 J (Peters 1983).

Table 2.3.1: ANCOVA tables of metabolism, ingestion, ingestion efficiency and interaction strength (continuous variables in italic and factors in bold). The metabolism ANCOVA does not include the factor "prey size".

		metabolism		ingestion		ingestion efficiency		short term interaction strength	
	d.f.	F	p	F	p	F	p	F	p
1: *Predator mass* (ln(M))	1	1012,23	< 0.001	341,43	< 0.001	13,61	< 0.001	1,23	0,27
2: **Temperature** (8°C / 15°C / 22°C)	2	326,35	< 0.001	6,38	< 0.01	63,87	< 0.001	1,43	0,24
3: **Prey size** (large / small)	1			1385,96	< 0.001	341,83	< 0.001	18,04	< 0.001
4: **Predator group** (beetles / spiders)	1	56,97	< 0.001	175,4	< 0.001	0,9	0.34	33,15	< 0.001
Predator mass x **Temperature**	2	0,08	0.92	1,36	0,25	2,27	0,11	2,39	0,09
Predator mass x **Prey size**	1			189,24	< 0.001	14,54	< 0.001	130,14	< 0.001
Temperature x **Prey size**	2			4,41	0.01	32,29	< 0.001	2,68	0,07
Predator mass x **Predator group**	1	26,04	< 0.001	7,35	< 0.01	0,04	0,84	28,14	0.001
Temperature x **Predator group**	2	0,88	0,41	1,53	0,22	0,68	0,51	3,53	0,03
Prey size x **Predator group**	1			47,32	< 0.001	1,68	0,2	< 0.01	0.96
1 x **2** x **3**	2			0,06	0,95	3,21	0,04	0,75	0,47
1 x **2** x **4**	2	0,13	0,88	0,59	0,56	0,62	0,54	1,5	0,23
1 x **3** x **4**	1			0,42	0,52	0.02	0,89	20,53	< 0.001
2 x **3** x **4**	2			0,97	0,38	0,26	0,77	3,39	0,04
1 x **2** x **3** x **4**	2			0,83	0,44	0,41	0,66	1,61	0,2

Residual standard errors are: metabolism (333), ingestion, ingestion efficiency and short term interaction strength (270)

For a subset of these predators we investigated how ingestion varied with predator and prey body mass, and temperature. Logistic constraints restricted our study to five beetle species (*Abax paralellepipedus*, *Carabus auratus*, *Platynus dorsalis*, *Poecilus versicolor* and *Pseudophonus rufipes*) and four spider species (*Alopecosa cuneata*, *Pardosa palustris*, *Pirata*

latitans and *Pisaura mirabilis*). For each predator species, the experiments were replicated six times: with large prey (beetle prey: fly larvae *Lucilia caesar*, spider prey: cricket *Gryllus sigillatus*) and with small prey (beetle prey: fruit fly *Drosophila hydei*, spider prey: springtail *Heteromurus nitidus*) in climatic chambers at three temperature levels (8°C, 15°C and 22°C). These two prey size groups represent the whole range of body size ratios found in nature (Brose, Jonsson, et al. 2006), including the left and right side of the hump-shaped relationship between predation rates and predator-prey body-mass ratios documented in a prior study (Brose et al. 2008). For both predator groups, we used two prey species with similar escape behaviour. Crickets and springtails avoid spider predation by jump-escaping in the case of emergency. Flightless fruit flies and the fly larvae escape beetle predation by crawling. Ingestion experiments were performed in 0.04 m² perspex arenas lined with dental cast to hold moisture during experimental time of 24 hours. Initially, we added 2.35g of re-moistened dry moss (*Polytrichum formosum*) as habitat structure, 30 prey individuals, N_i, and one predator individual to each arena. The number of the remaining prey individuals was counted after 24 hours to calculate the number of prey individuals eaten (N_e). The full-factorial combination of the independent variables (nine predators, two prey sizes, three temperatures) with six replicates per combination resulted in a total of 324 experimental units.

For every combination of predator j and prey i, we calculated the ingestion rate, J_{ij} [J/s],

$$J_{ij} = \frac{N_e M_i \varepsilon}{t_F} \qquad (2.3.1a)$$

where M_i is the individual body mass of a prey individual [g/Ind.] and t_F is the experimental duration in [s], we assume an energy content ε of 7000 J/g wet mass (Peters 1983). Subsequently, we calculated the dimensionless ingestion efficiency (Vasseur and McCann 2005) as

$$y_{ij} = \frac{w_{ij} J_{ij}}{\lambda I_j} \qquad (2.3.1b),$$

where w_{ij} is the dimensionless assimilation efficiency ((ingestion – faeces)/ingestion). We assumed a constant assimilation efficiency (w_{ij} = 0.85, (Lawton 1970; Peters 1983; Yodzis and Innes 1992)) that does not vary with environmental temperature as documented in most empirical studies, e.g. of carnivorous insects (Lawton 1970), caterpillars (Kingsolver and Woods 1998) and lizards (Chen et al. 2003; McConnachie and Alexander 2004). λ is a dimensionless constant converting basal metabolic rate into field metabolic rate (λ=3 (Savage, Gillooly, Brown, et al. 2004)), and I_j is the metabolic rate of predator j (calculated according to Eqn. 2.3.2a below). The ingestion efficiency expresses the ingestion gain of a consumer relative to its metabolic loss, and it is thus closely related to biomass gains or losses.

While there is a wide range of different metrics that can be used to calculate *per capita* interaction strengths (Berlow et al. 2004, 1999), we focused on the most widely used: the log response ratio, (Berlow et al. 1999; Emmerson and Raffaelli 2004):

$$\alpha_{ij} = \left| \frac{\ln\left((N_i - N_e)/N_i \right)}{t} \right| \qquad (2.3.1c),$$

where t [days] is the experimental duration, N_i [Ind.] is the initial prey abundance and N_e [Ind.] is the number of prey eaten. In our case, the short term interaction strength is the log ratio between the prey abundances at the end and at the start of the experiment. This approach assumes that prey abundance without predators equals the initial prey density, and that thus natural mortality of the prey species is negligible. This assumption was supported by the lack of mortality in controls without predators.

Statistical analysis of experimental data

All data were analysed by ANCOVAs with the statistical software R 2.9.0 (R Development Core Team 2009) to distinguish between effects of the factors (1) predator group (beetle or spider) and (2) prey size (large or small, only for ingestion experiments), (3) level of environmental temperature (8°C, 15°C, 22°C), and the continuous variable (4) predator mass [ln(g)]. Subsequently, we generated multiple regression models following the MTE (Brown et al. 2004) predicting that *per capita* rates of metabolism, I_j [J/s], and ingestion, J_{ij} [J/s], of an ectotherm organism depend on its body mass, M [g], and the environmental temperature, T [K] as:

$$I_j = i_0 M_j^{b_I} e^{\frac{-E_I}{kT}} \qquad (2.3.2a)$$

$$J_{ij} = j_0 M_j^{b_J} e^{\frac{-E_J}{kT}} \qquad (2.3.2b)$$

where i_0 and j_0 are normalisation constants, b is an allometric exponent, k is Boltzmann's constant (8.62 x 10^{-5} eV/K) and E [eV] is the activation energy. In the same vein, we analysed the temperature and body-mass dependence of ingestion efficiencies and interaction strengths as:

$$y_{ij} = y_0 M_j^{b_y} e^{\frac{-E_y}{kT}} \qquad (2.3.2c),$$

$$e^{\alpha_{ij}} = \alpha_0 M_j^{b_\alpha} e^{\frac{-E_\alpha}{kT}} \qquad (2.3.2d).$$

Note that due to the fact that the per capita interaction strength is calculated as the natural logarithm (Eqn.. 2.3.1c), we used the exponential functions for investigating the mass and temperature dependence of per capita interaction strength (Eqn. 2.3.2d). Consistent with prior studies (Brown et al. 2004; Meehan 2006a, b), we made multiple linear least-squares regressions with the GLM-procedure of the statistical software R 2.9.0 (R Development Core Team 2009) to estimate the parameters of equation (2.3.2a-d) after ln-transformation.

Long Term Interaction Strength

Calculations of long term interaction strengths were based on a population dynamic model (Rall et al. 2008; Vasseur and McCann 2005; Yodzis and Innes 1992) of prey density, N [Ind/m²], and predator density, P [Ind/m²]:

$$\frac{dN}{dt} = r\left(1-\frac{N}{K}\right)N - c_J J_{ij} N P \qquad (2.3.3a),$$

$$\frac{dP}{dt} = \frac{c_J J_{ij} N P}{w_{ij}} - c_I I_j P \qquad (2.3.3b),$$

where t [days] is time, r [1/day] is the intrinsic growth rate, and K [Ind/m²] is the carrying capacity of the prey species. The feeding interaction follows a linear functional response, where J_{ij} [J/s] is the ingestion rate of a single predator, c_J [s N day^{-1} J^{-1}] is a correction factor that converts the ingestion rate from Joules per second into prey individuals per day. I_j [J/s] is the metabolic rate of the predator and c_I is a correction factor that converts metabolism from Joules per second into predator individuals per day [s P day^{-1} J^{-1}]. The temperature and mass dependent intrinsic growth rate r in (2.3.3a) is calculated by

$$r = r_0 M^{b_r} e^{\frac{E_r}{kT}} \qquad (2.3.4a),$$

where r_0 (r_0=e$^{32.39}$, Savage, Gillooly, Brown, et al. 2004) is a normalisation constant, M is the mass [µg], b_r (b_r=-0.25) is a constant exponent, k is Boltzmann's constant (8.62 x 10^{-5} eV/K) and E_r (-0.84 eV) is the activation energy for insects (Savage, Gillooly, Brown, et al. 2004).

The carrying capacity K in (2.3.3a) depends on environmental temperature, body mass, the trophic level of the prey and the net primary production of the habitat (Allen et al. 2002, 2006) following

$$K = K_0 m^{b_K} e^{\frac{E_K}{kT}} \sigma^z e^{tl_0(tl-1)} \qquad (2.3.4b),$$

where K_0 is a normalisation constant, b_K is a constant exponent, E_K is the activation energy, σ is the annual net primary productivity of the habitat [g(C) m^{-2} y^{-1}], z is a constant exponent, tl_0

is a constant and *tl* the trophic level. We used constants found in other studies with similar soil invertebrates as in our study: $K_0 = e^{-31.15}$; b_K =-0.72; E_K = 0.71; tl_0 = -2.68; z = 1.03; tl = 1.5 for decomposers, fungivores and herbivores (Meehan 2006b). The net primary productivity in (2.3.4b) is temperature dependent (Allen et al. 2005):

$$\sigma = \sigma_0 e^{\frac{E_\sigma (T_0 - T)}{kTT_0}} \qquad (2.3.4c),$$

where σ_0 is the net primary productivity at the temperature T_0 [K] and E_σ is the activation Energy (-0.35 eV, of the net primary production that is mechanistically derived from the activation energy of photosynthesis (Allen et al. 2005)). We assumed an average net primary production, σ_0, of 600 g(C) m^{-2} y^{-2} for temperate regions (Cramer et al. 1999) at an average temperature T_0 of 9.5°C (282.65 K) which is approximately equal to the annual average temperature in Germany since 2000 (Deutscher Wetterdienst 2007).

The long term population densities of (2.3.3a, b) are calculated assuming that the system is at equilibrium (i.e. dN/dt = 0; dP/dt = 0), which yields equilibrium densities (P', N') of

$$P' = \frac{(K - N')r}{c_J J_{ij} K} \qquad (2.3.5a),$$

$$N' = \frac{w_{ij} c_I I_j}{c_J J_{ij}} \qquad (2.3.5b).$$

Subsequently, the long term *per capita* interaction strength between i and j, A_{ij}, is calculated according to the log ratio interaction strength used in prior studies (also known as dynamic index) (Berlow et al. 1999; Emmerson and Raffaelli 2004):

$$A_{ij} = \left| \frac{\ln\left(N^+ / N^-\right)}{Y} \right| \qquad (2.3.6),$$

where N^+ is the prey abundance when the predator is present and N^- is the prey abundance when the predator is absent and Y is the predator abundance. We can replace N^+ by N' and Y by P' (see Eqn. 2.3.5a, b). Moreover, in absence of a predator the prey is growing to its carrying capacity (Eqn. 2.3.4b), and we can replace N^- with K, which yields

$$A_{ij} = \left| \frac{\ln\left(N'/K\right)}{P'} \right| \qquad (2.3.7).$$

Inserting the equations 2.3.5a and 2.3.5b in equation 2.3.7 and using the temperature dependencies of I_j (Eqn. 2.3.2a), J_{ij} (Eqn. 2.3.2b), K (Eqn. 2.3.4b) and r (Eqn. 2.3.4a) yields the long-term interaction strengths depending on environmental temperature.

d) Results

Respiration and ingestion experiments

The metabolic rates of the predators, beetles and spiders, increased significantly with their body mass and temperature (Fig 2.3.1 a, b; ANCOVA, Table 2.3.1). The significant interaction term between predator mass and predator group (Table 2.3.1) suggests that the exponent for beetles (b_I = 0.72; Table 2.3.2; Fig. 2.3.1a, circles) is higher than the exponent for spiders (b_I = 0.46; Table 2.3.2; Fig. 2.3.1a, crosses). In contrast, the interaction term between temperature and predator group was not significant (Table 2.3.1) suggesting that the activation energy was similar for beetles (E_I = 0.87; Table 2.3.2; Fig. 2.3.1b, circles) and spiders (E_I = 0.80; Table 2.3.2; Fig. 2.3.1b, crosses).

We found significant effects of predator body mass and temperature on ingestion rates (ANCOVA, Table 2.3.1). Significant interaction terms with predator mass indicate that the allometric exponents differ for predator groups and prey size (Table 2.3.1): exponents were higher for beetles than for spiders and while ingestion increased with predator body mass when prey were large (b_J = 0.82 and b_J = 0.6 for beetles and spiders, respectively; Table 2.3.2; Fig. 2.3.1c), it decreased with predator body mass when prey were small (b_J = -0.25 and b_J = -0.63 for beetles and spiders, respectively; Table 2.3.2; Fig. 2.3.1e). Temperature effects on ingestion were similar for both predator groups (no significant interaction term between temperature and predator group) while they differed with respect to prey size (Table 2.3.1). Ingestion increased with temperature when prey were large (E_I = 0.24 and E_I = 0.30 for beetles and spiders, respectively; Table 2.3.2; Fig. 2.3.1d), whereas it did not vary significantly when

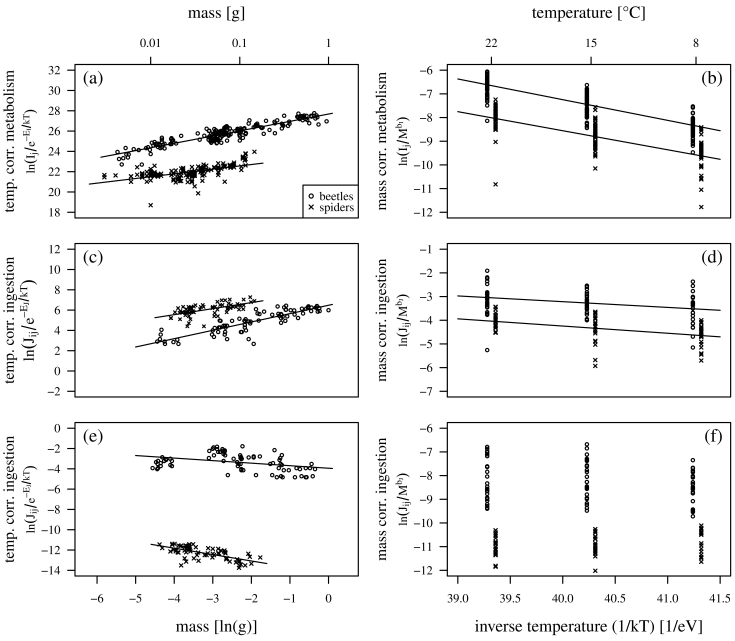

Figure 2.3.1: Beetle (circles) and spider (crosses) metabolism I_j **(a, b)**, ingestion J_{ij} of the larger **(c, d)** and the smaller prey (e, f) depending on predator body mass **(a, c, e)** and environmental temperature (b, d, f). Data are ln-transformed and the dependent variables are normalised by their temperature dependence **(a, c, e)** or their mass dependence **(b, d, f)**. Upper axes show untransformed body mass [g] and temperature [°C] scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels **b)**, **d)** and **f)**. Note the inverse scaling of the lower temperature axes.

prey were small (Table 2.3.2; Fig. 2.3.1f).

Table 2.3.2: Regression results for the body-mass and temperature dependence of metabolism, ingestion, ingestion efficiency and interaction strength.

	ln(*c*)	p	lower CI	upper CI	*b*	p	lower CI	upper CI	*E*	p	lower CI	upper CI	r²	AIC	n
metabolism															
beetles	27.68	***	24.72	30.64	0.72	***	0.68	0.77	0.87	***	0.80	0.95	0.89	192.19	183
spiders	23.62	***	19.17	28.07	0.46	***	0.36	0.55	0.80	***	0.69	0.91	0.64	265.06	162
ingestion of large prey															
beetles	6.47	*	0.13	12.82	0.82	***	0.71	0.93	0.24	**	0.09	0.40	0.75	142.11	80#
spiders	7.93	*	2.05	13.81	0.60	***	0.40	0.79	0.30	***	0.16	0.45	0.42	96.26	67#
ingestion of small prey															
beetles	-3.94	-	-12.86	4.97	-0.25	**	-0.39	-0.11	0.11	-	-0.11	0.33	0.14	193.17	79#
spiders	-14.34	***	-20.19	-8.48	-0.63	***	-0.80	-0.46	-0.09	-	-0.23	0.06	0.44	97.04	68#
ingestion efficiency – large prey															
beetles	-22.40	***	-28.74	-16.05	0.10	-	-0.01	0.21	-0.63	***	-0.79	-0.47	0.47	142.23	80#
spiders	-16.88	***	-22.77	-10.99	0.14	-	-0.06	0.33	-0.50	***	-0.64	-0.36	0.45	96.48	67#
ingestion efficiency – small prey															
beetles	-32.84	***	-41.76	-23.92	-0.97	***	-1.11	-0.83	-0.76	***	-0.99	-0.54	0.74	193.28	79#
spiders	-39.18	***	-45.03	-33.32	-1.09	***	-1.26	-0.91	-0.89	***	-1.03	-0.74	0.81	97.17	68#
absolute interaction strength with large prey															
beetles	3.33	***	1.46	5.20	0.16	***	0.13	0.19	0.07	**	0.02	0.11	0.58	-53.29	80#
spiders	3.62	***	2.19	5.05	0.15	***	0.11	0.20	0.07	***	0.04	0.11	0.44	-92.85	67#
absolute interaction strength with small prey															
beetles	2.80	*	0.22	5.39	-0.04	-	-0.08	0.00	0.07	*	0.00	0.13	0.09	-2.55	79#
spiders	-5.13	*	-8.95	-1.31	-0.36	***	-0.48	-0.25	-0.11	*	-0.21	-0.02	0.4	38.99	68#

c = normalization constant; p = level of significance; CI = confidence interval; *b* = allometric exponent; *E* = activation energy; # = zero values omitted for ln transformation. Level of significance: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Ingestion efficiency:

From the metabolism and ingestion measures, we calculated the ingestion efficiency (ingestion / metabolism) for each predator. We found significant effects of temperature and predator body mass on ingestion efficiencies (ANCOVA, Table 2.3.1). Significant interaction terms indicated that these effects depend on prey type, whereas non-significant interaction terms suggest similar mass and temperature effects for both predator groups (ANCOVA, Table 2.3.1). For both predator groups, ingestion efficiencies did not vary with predator mass in treatments with large prey (Fig. 2.3.2a; Table 2.3.2), whereas they decreased in treatments with small prey (Fig. 2.3.2c; Table 2.3.2). Eventually, ingestion efficiencies fell below unity

indicating that metabolism exceeded ingestion (Fig. 2.3.2c, red symbols). For both predator groups and both prey sizes, increasing temperature generally decreased the ingestion efficiency, which increased the number of predator individuals that could not balance their metabolic demands (Fig. 2.3.2b, d, red symbols; 8°C: 11 individuals, 15°C: 20 individuals, 22°C: 34 individuals). Thus, the critical boundary, at which predator ingestion was insufficient to balance metabolic loss ($y_{ij} < 1$, Eqn. 2.3.1b) shifted to a range of lower predator body masses when temperature increased.

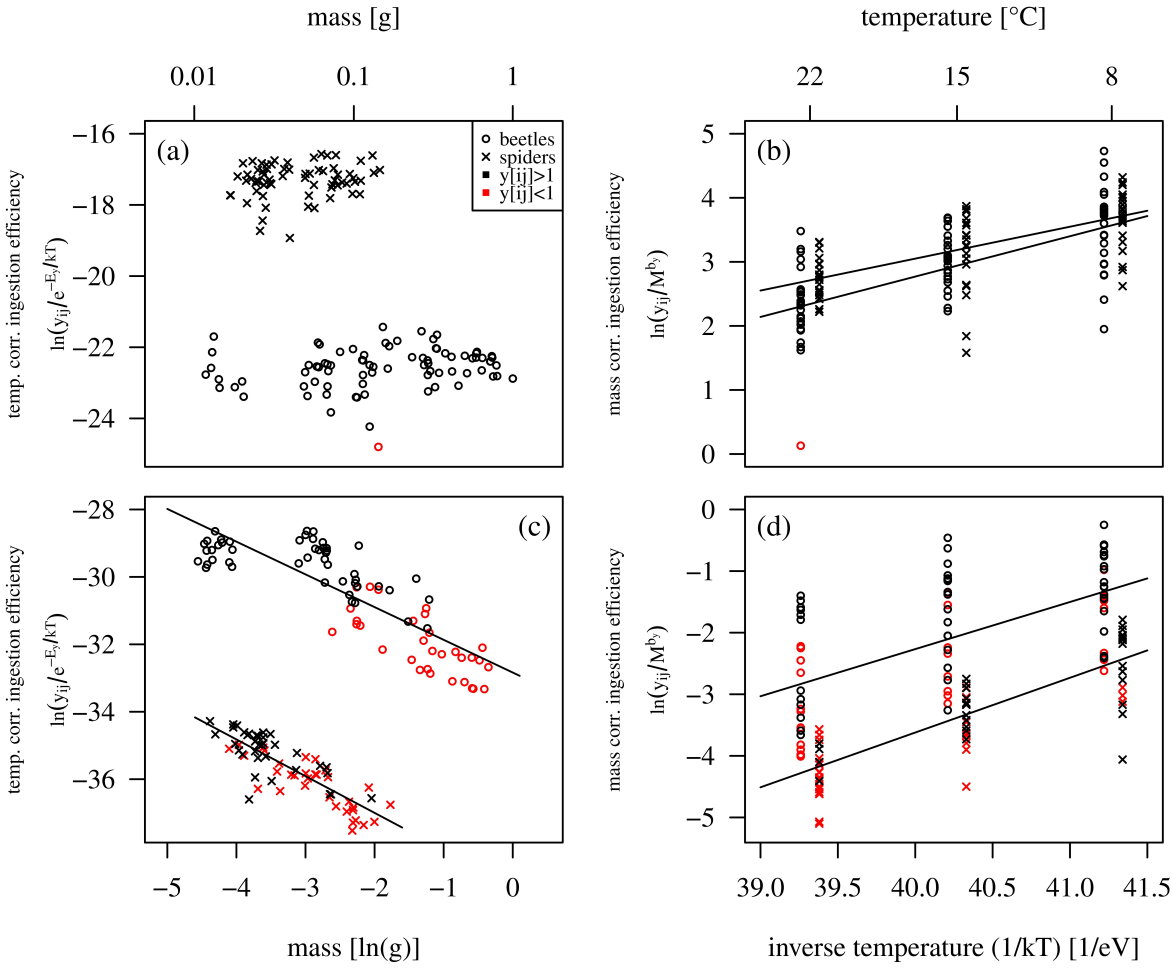

Figure 2.3.2: Beetle (circles) and spider (crosses) ingestion efficiency y_{ij} in treatments with the larger **(a, b)** and the smaller prey **(c, d)** depending on predator body mass **(a, c)** and environmental temperature **(b, d)**. Data are ln-transformed and the dependent variables are normalised by their temperature dependence **(a, c)** or their mass dependence **(b, d)**. Upper axes show untransformed body mass [g] and temperature [°C] scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels **b)** and **d)**. Note the inverse scaling of the lower temperature axes. Red coloured circles and crosses indicate where the ingestion efficiency was below the critical threshold of unity ($y_{ij} < 1$).

Short term interaction strength:

Effects of predator mass and temperature on short-term interaction strengths exhibited a significant dependence on predator group and prey size (significant three-way interaction terms in Table 2.3.1). Short-term interaction strengths increased significantly with predator body mass in treatments with large prey irrespective of the predator group (Fig. 2.3.3a). In treatments with small prey, short-term interaction strengths decreased slightly with predator mass for spiders, but they remained constant for beetles (Fig. 2.3.3c; Table 2.3.2). Moreover, short-term interaction strengths increased with warming when predators fed on large prey (Fig. 2.3.3b; Table 2.3.2) and when beetles fed on small prey (Fig. 2.3.3d, circles; Table 2.3.2). In contrast, short-term interaction strengths decreased slightly with warming when spiders fed on small prey (Fig. 2.3.3d, crosses; Table 2.3.2).

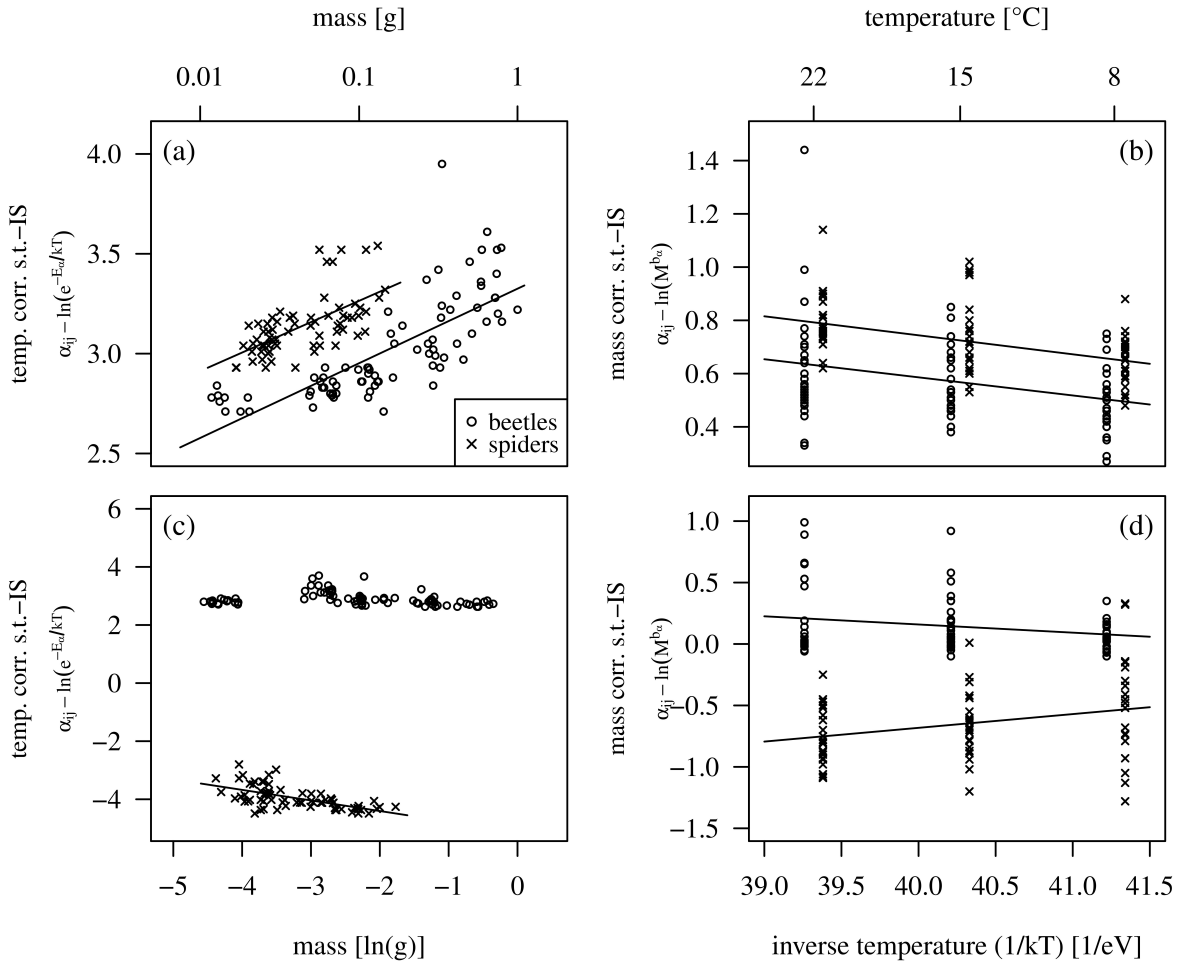

Figure 2.3.3: Beetle (circles) and spider (crosses) absolute short term per capita interaction strength α_{ij} in treatments with the larger **(a, b)** and the smaller prey **(c, d)** depending on predator body mass **(a, c)** and environmental temperature **(b, d)**. Data are ln-transformed and the dependent variables are normalised by their temperature dependence **(a, c)** or their mass dependence **(b, d)**. Upper axes show untransformed body mass [g] and temperature [°C] scales. Offsets of -0.04 (beetles) and 0.04 (spiders) were applied to temperature data in panels **b)** and **d)**. Note the inverse scaling of the lower temperature axes.

Prediction of long term interaction strength

Calculated long-term interaction strength generally decreased with increasing temperature across all combinations of predator groups, predator masses and prey sizes (Fig. 2.3.4). Large predators have a higher impact on the large prey and smaller predators have a higher impact on the small prey (Fig. 2.3.4a & b vs. Fig. 2.3.4c & d). In all cases, the total decrease in long-term interaction strength is stronger when the long-term interaction strength is generally strong (Fig. 2.3.4).

e) Discussion

Consistent with the MTE (Brown et al. 2004), our experiments demonstrate that the metabolism of beetles and spiders followed a power-law increase with their body mass and an exponential increase with temperature. However, we did not find similar relationships for predator ingestion rates. As expected based on recent foraging studies documenting hump-shaped relationships between ingestion and predator-prey body-mass ratios (Brose et al. 2008; Vonesh and Bolker 2005; Wahlström, Persson, Diehl, and Byström 2000), we found differences in warming effects on ingestion rates between treatments with small prey (constant

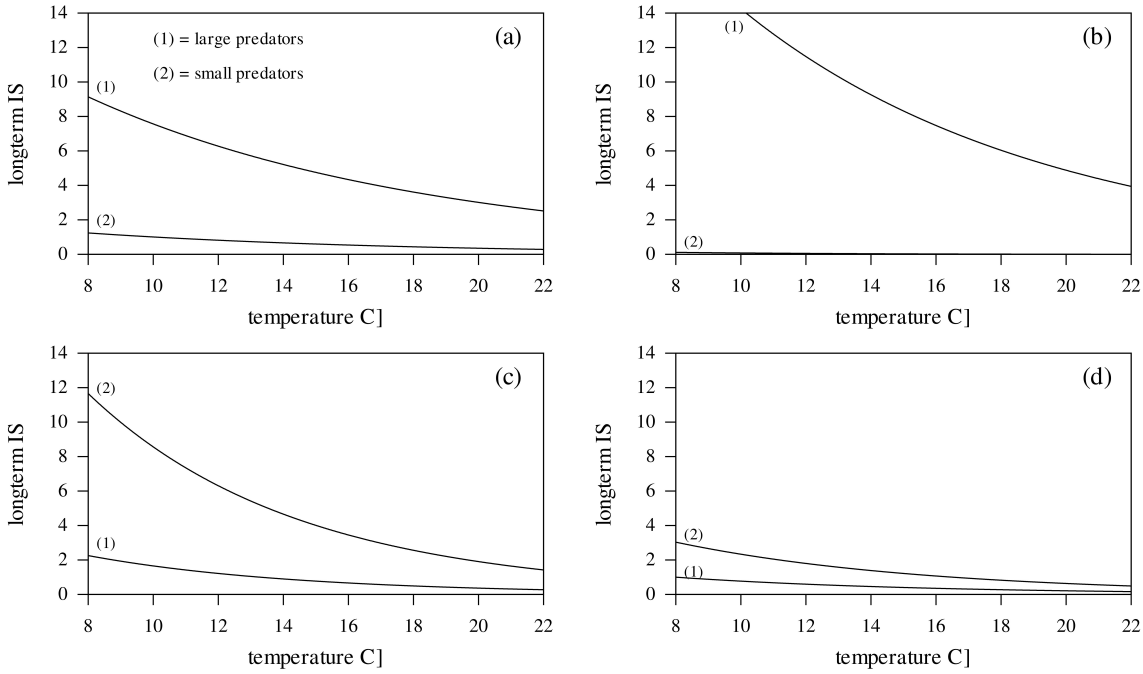

Figure 2.3.4: Beetle **(b, d)** and spider **(a, c)** long term per capita interaction strength A_{ij} in treatments with the larger **(a, b)** and the smaller prey **(c, d)** in dependence on environmental temperature. Lines marked with (1) denote largest predators in our experiments (beetles: 1000 mg, spiders: 170 mg) and lines marked with (2) denote smallest predators in our experiments (beetles: 11 mg, spiders: 13 mg).

rates) and treatments with large prey (increasing rates). In contrast to our initial expectation based on the MTE, activation energies of ingestion were lower than those of metabolism, and thus ingestion efficiencies (the ratio of ingestion to metabolism) generally decreased with warming. Moreover, short-term interaction strengths (only accounting for ingestion) increased with warming in all treatments except for the treatment with spiders and small prey, whereas the long-term interaction strengths (additionally accounting for temperature effects on prey abundance) generally decreased. Together, these results demonstrate that warming may have complex and profound implications for predator-prey interaction strengths, population dynamics and food-web stability.

Metabolism

The MTE predicts a 3/4 power-law increase in metabolism with body mass and an exponential increase with temperature, where the activation energy should be in the range of biochemical reactions between 0.2 and 1.4 eV (Clark et al. 2004; Gillooly et al. 2001). Generally, most of our results corroborate the predictions of the MTE. The exception is spider metabolism, which exhibited a particularly low allometric exponent (b_I = 0.46±0.09). The low spider exponent may be caused by factors limiting metabolism other than the circulatory transport network (e.g. the relative metabolic tissue is larger in small than in large spiders; but see (Brose et al. 2008) for more examples), but a mechanistic explanation of allometric exponents is beyond the scope of this study.

Body-mass effects on ingestion

Following assumptions of the MTE, the allometric exponents and the activation energies for ingestion should be similar to those for metabolism (Brown et al. 2004). Consistent with this assumption, the allometric exponents for metabolism were within the 95% confidence intervals of those for ingestion in treatments with large prey. Moreover, the confidence intervals of the allometric exponents of both predator groups in treatments with large prey include the 3/4 exponent predicted by models based on MTE (Brown et al. 2004). Contrary to the assumptions of the MTE, however, the allometric exponents of ingestion in treatments with small prey were negative, indicating that ingestion rates decreased with increasing predator body mass.

The pattern of increasing and decreasing ingestion rates documented here is consistent with hump-shaped relationships between ingestion and predator-prey body-mass ratios documented by foraging theory (Brose et al. 2008; Vonesh and Bolker 2005; Vucic-Pestic et al. 2010; Wahlström, Persson, Diehl, and Byström 2000). On the left side of the hump at low body-mass ratios (e.g., large prey in our experiments), predator effects on prey are limited by

handling-time constraints and ingestion rates increase with body-mass ratios due to decreasing handling time (i.e. the disparity in predator and prey body mass increases and large predators are able to handle small prey with ease). On the right side of the hump, when body-mass ratios are large (e.g. small prey in our experiments), predator ingestion is constrained by the rate at which they can catch small prey and ingestion rates decrease with body-mass ratios, because the predators' attacks become increasingly inefficient (Aljetlawi et al. 2004; Brose et al. 2008). Predators may either not perceive prey, or there is a trade off between the time taken to capture a very small prey item and the energetic benefit derived from the interaction. Thus, the effects of increasing predator body-mass on ingestion should deviate from a simple power law when a wider range of predator and prey body masses is considered. As in prior studies over a more limited range of body-mass ratios (Emmerson and Raffaelli 2004; Peters 1983), we found that the increasing slope of this hump-shaped relationship at low body-mass ratios (i.e. large prey) is well described by an increasing power function. However, documentation of a hump-shaped relationship required extension of the range of body-mass ratios studied to include decreasing ingestion rates at high body-mass ratios (i.e. small prey in our study).

Temperature effects on ingestion, ingestion efficiencies and interaction strengths

The activation energies of ingestion were more than two times smaller than those of metabolism. Thus, the response of ingestion to warming is much weaker than the increase in metabolism. Contrary to expectations based on the MTE, ingestion efficiencies (i.e. ingestion relative to metabolism) thus decreased with warming independent of the prey size and predator group. Eventually, warming leads to ingestion efficiencies below unity (ingestion lower than metabolic demands, see Figure 2.3.2, red symbols), which causes predator starvation. This suggests that many predator-prey interactions could become infeasible under warming. The activation energies of ingestion were slightly positive in treatments with large prey where predators were limited by handling time, which includes biochemical digestion processes (van Rijn et al. 2005). Warming can accelerate these biochemical processes (Gillooly et al. 2001), which leads to faster handling time thus explaining higher ingestion rates in our experiments with large prey. Interestingly, the activation energies of ingestion were not significantly different from zero in treatments with small prey, where predators were constrained by their ability to catch prey, and ingestion was independent of digestion and satiation (van Rijn et al. 2005). Warming does not affect the catching efficiency, which is primarily driven by constraints such as detectability and mobility. If warming had an equal effect on predator and prey mobility, the net effect of warming on the catching efficiency of predators would be neutral, which could explain the lack of warming effects in our treatments with small prey.

Generally, absolute short term *per capita* interaction strengths increased with temperature

except for the treatment of spiders with small prey. This corroborates a prior field study documenting positive effects of temperature on interaction strengths in a marine intertidal food web (Sanford 1999). Our study demonstrates that these positive temperature effects are driven by increasing ingestion rates. While comprehensive field studies investigating temperature and body-mass effects on interaction strengths are scarce, based on metabolic arguments our study suggests the broad generality of positive correlations between temperature and short term interaction strengths.

Interestingly, the absolute values of the long term interaction strengths (not taking its sign into account) decrease with warming. This is caused by differences between the activation energies of predator metabolism and ingestion (see Eqn. 2.3.5b) yielding higher prey population densities at higher temperatures in simple predator-prey systems. Moreover, the carrying capacity of the prey decreases because abundances of natural populations embedded in a complex network generally decrease with warming (Allen et al. 2002; Meehan 2006b). The long-term interaction strengths (Eqn. 2.3.6) are proportional to the ratio of the equilibrium prey density (increasing with warming) to the prey carrying capacity (decreasing with warming). Consequently, this ratio increases with warming, yielding less negative values, and decreases in absolute strength. Additionally, due to the differences in prey growth rates and predator ingestion rates, the predator density increases with warming causing an additional decrease in absolute *per capita* interaction strength with warming (Eqn. 2.3.5a).

While short-term interaction strengths were determined by increases in predator ingestion rates under warming (see Eqn. 2.3.1c), temperature effects on predator and prey densities outweigh these increasing ingestion rates and yield decreasing long-term interaction strengths under warming. This disparity between different measurements of interaction strength on different time scales is a general problem in ecological sciences, especially in experiments exploring aspects of climate change (Walther 2007). The approach adopted in this study to calculate long-term interaction strengths might offer a solution to this problem.

Temperature effects on population stability:

In our experiments, ingestion rates and short term interaction strengths with large prey (low body-mass ratios) increased with warming. This may result in a stronger short-term top-down control of prey populations under warming when prey growth rates and densities are negligible. However, long-term interaction strengths generally decrease with warming. As decreasing interaction strengths are inversely correlated with perturbation stability (May 1972), our results suggest that the perturbation stability of natural communities should increase with warming. Additionally, our results demonstrate decreases in ingestion efficiencies with warming, which should lead to higher intrinsic population stability for all predator-prey interactions irrespective of the body-mass ratio (Rall et al. 2008; Vasseur and

McCann 2005; Yodzis and Innes 1992). However, decreased ingestion efficiencies combined with higher predator density may lead to starvation of the predator population, even if the prey population also has increased in density. Consistent with this conclusion, warming of microcosm food webs caused an increase in biomass of bacteria and bacteriovorus consumers whereas larger predators and herbivores became extinct and the biomass of producers increased (Petchey et al. 1999). Our results indicate that predator-prey interactions characterised by high body-mass ratios (small prey in our experiments) are particularly prone to this predator-starvation effect of warming. Analyses of the body-mass structure of natural food webs (Brose, Jonsson, et al. 2006) may thus facilitate predictions of their sensitivity to global warming. Global warming may also increase the productivity of ecosystems because of increasing CO_2 levels (Emmerson et al. 2005), which may counteract the direct temperature effects studied here due to increased net primary productivity. Eventually, these two global warming effects need to be reconciled to achieve accurate forecast models.

Caveats

As any laboratory study, our approach was based on some simplifying assumptions: (1) simple predator-prey pairs ignore potentially more complex feeding behaviour of predators when multiple prey or predator species or multiple predator individuals coexist (e.g., prey switching or interference competition, compensatory effects of alternative predators); (2) constant prey densities across all ingestion experiments do not account for non-linearly saturating responses of ingestion to high prey densities. Future more complex extensions of our laboratory approach will need to address effects of these simplifying assumptions. However, our assumption of constant assimilation efficiencies across the temperature gradient is supported by empirical studies of carnivorous insects (Lawton 1970), caterpillars (Kingsolver and Woods 1998) and lizards (Chen et al. 2003; McConnachie and Alexander 2004). As most prior warming experiments, our approach did not account for thermal adaptation of the species, which can reduce their physiological responses to warming (Lenski and Benett 1993). However, a 76% lower activation energy of metabolism as documented for fish species after thermal adaptation (Clarke and Johnston 1999) would not affect the qualitative conclusions of the present study. Nevertheless, our approach presents a simplistic, mechanistic null model of temperature effects on predator-prey interactions in which thermal adaptation effects remain to be included. In contrast, prior, long-term field studies on the effects of warming avoid some of these simplifying assumptions at the cost of lacking mechanistic explanations. Future studies will need to bridge the gap between simplified but mechanistic laboratory studies and more complex field studies.

Conclusions

Four conclusions arise from our results: warming of natural ecosystems may cause (1) higher feeding rates and short term interaction strengths yielding higher impacts on a prey population over a short period of time, (2) higher perturbation stability of the populations (higher probability of returning to the same equilibrium density after a small perturbation) due to lower absolute long-term *per capita* interaction strengths, (3) a higher intrinsic population stability (less fluctuations in population density) due to reduced ingestion efficiencies, and (4) higher extinction risks due to predator starvation. As species interactions provide the mechanistic link between global warming and ecosystem functions (Hughes 2002), our results suggest that predicting the consequences of climate change may be far from trivial. Nevertheless, future extensions of our approach may provide a mechanistic understanding of how warming affects population dynamics, species' extinction risks and ecosystem functions.

2.4. Prey mobility constrains warming effects on interaction strengths

a) Abstract

Global warming is commonly accepted and scientific research increased in the last few years on this subject. To understand the effect of increasing temperatures on ecosystems and on their populations, it is necessary to understand how warming affects the interaction strengths between predators and prey. We studied the functional response of three different carabid beetles of different sizes with one resident (*Alphitobius diaperinus*) and one mobile (*Drosophila hydei*) prey at six different temperatures (5, 10, 15, 20, 25 and 30 °C) in a laboratory system. Further more, we investigated how the metabolism of the predators changed at the investigated temperatures and if the temperature dependencies were influenced by the body mass. Finally, we calculated the energetic efficiency (ingestion/metabolism) as a function of increasing temperature.

We showed that temperature increased the metabolism and the per capita consumption rates of the beetles. Handling time was negatively correlated with temperature, while search rates increased only for the mobile prey. Additionally, metabolism and handling time were affected by body mass. Energetic efficiency decreased with temperature, although it was more pronounced for the smaller mobile prey (due to lower energy content of the prey). Together our results suggest that warming has a complex effect on the nonlinear interaction strengths investigated in this study and consequently on the food web-stability of the investigated terrestrial system.

We demonstrated for the first time to our knowledge that the increase in attack rates under warming depends on the mobility pattern of the prey. We showed that when predators preyed on mobile prey the attack rates increased with warming whereas the attack rates remained unaffected when the same predator preyed on resident prey. This study contributes to a better understanding of how changes in temperature affect predator-prey interactions, by presenting a concept that differentiates between metabolic driven effects on handling times and behavioural effects on the attack rates.

We present a mechanistic framework that may allow making detailed predictions on the warming induced changes on predator-prey interaction strengths depending on metabolic and behavioural constrains.

b) Introduction

Environmental warming can have complex and potentially catastrophic consequences for natural ecosystems . For instance, warming can directly affect population physiological rates and abundances (Hughes 2000; Parmesan 2006). These direct effects are conceptualized by the metabolic theory of ecology holding that the rates of metabolism and many other biological processes increase exponentially with environmental temperature (Gillooly et al. 2001). Additionally, warming can impose indirect effects on populations via variation in interaction strengths with coexisting species, which can severely impact food-web stability (Berlow et al. 2004, 2009; Neutel et al. 2002; O'Gorman and Emmerson 2009; de Ruiter et al. 1995), but understanding how warming affects interaction strengths remains elusive.

A simple mechanistic model of non-linear predator-prey interaction strengths is provided by functional responses of *per capita* ingestion rates, F, depending on prey density, N:

$$F = \frac{aN}{1 + ahN} \tag{2.4.1}$$

where a is the attack rate (i.e., rate of successful capture, hereafter: attack rate), and h is the handling time needed to kill, ingest and digest a resource individual (Holling 1959c) Recently, interest in these parameters has been invigorated by their central importance for an allometric model predicting the network structure of food webs (Petchey et al. 2008). Dynamically, limited variation in their parameters can have dramatic consequences for population and food-web stability (Brose, Williams, et al. 2006; Oaten and Murdoch 1975; Rall et al. 2008; Williams and Martinez 2004). In particular, depending on the relative strength of warming effects on ingestion and metabolism, it can lead to stabilization or destabilization of population and food web dynamics (Vasseur and McCann 2005).

Metabolically derived null expectations suggest that maximum ingestion rates (the inverse of handling time) should exhibit a similar temperature dependence as the metabolic rates, which should yield exponential decreases in handling time under warming. While most empirical studies supported this negative relationship between handling time and environmental temperature, they also documented that the scaling of attack rates with warming can follow linear, power-law, sigmoid, or hyperbolic increases, it can be dome-shaped or entirely absent (Bailey 1989; Bergman 1987; Cave and Gaylor 1989; Dreisig 1981; Garcia-Martin et al. 2008; Gilioli et al. 2005; Gresens et al. 1982; McCoull et al. 1998; Song and Heong 1997; Thompson 1978; Xia et al. 2003; Zhang et al. 1999, 1998). This plethora of scaling relationships precludes any general conclusions on how warming affects interaction strengths.

We propose the following general concept for understanding warming effects on attack

rates: (1) attack rates are directly proportional to encounter rates, e, and success rates, s, (here, we assume for the sake of simplicity that encounters lead to attacks), (2) encounter rates depend on predator and prey movement speed, $m_{i,j}$, (3) success rates are inversely proportional to prey escape efficiencies, ϵ, and (4) $m_{i,j}$, and ϵ follow exponential temperature scaling:

$$a = e\ s = m_i m_j / \epsilon \approx e^{\frac{E_1}{kT}} e^{\frac{E_2}{kT}} e^{\frac{-E_3}{kT}} = e^{\frac{(E_1 + E_2 - E_3)}{kT}} \quad , \qquad (2.4.2)$$

where k is Boltzmann's constant, T is temperature [K], and E_1, E_2, E_3 are the activation energies of m_i, m_j and ϵ, respectively. Together, this suggests a twofold positive effect of predator and prey mobility (E_1, E_2) on encounter rates and a simple negative effect on attack success rates (E_3), which should result in increases in attack rates under environmental warming (if $E_1 + E_2 > E_3$). However, a different prediction arises if the prey species (or the predator) is resident (i.e., of limited mobility) and does not respond to warming ($E_2 \sim 0$), which should yield attack rates that are roughly independent of environmental temperature (if $E_1 \sim E_3$). This concept suggests that prey mobility should constrain warming effects on interaction strengths.

Recently, we demonstrated systematic effects of predator and prey body masses on functional response parameters for terrestrial invertebrate predators (Brose et al. 2008). Here, we extended these analyses by choosing three predators along the body-mass gradient to study effects of environmental temperature on their metabolic rates and functional responses. For the first time, the combined analyses of metabolism and functional responses allowed calculating warming effects on ingestion efficiencies (ratio of ingestion to respiration). To address constraints of prey mobility, we replicated the functional response experiment with one mobile and one resident prey.

c) Methods

Experiments

We studied the functional responses of three differently-sized predators (*Pterostichus melanarius, Harpalus rufipes, Calathus fuscipes,* Carabidae: Coleoptera) on one mobile (flightless adults of *Drosophila hydei*; Diptera; Drosophilidae, hereafter: *Drosophila*) and one resident prey (*Alphitobius diaperinus*; Coleptera; Tenebrionidae; hereafter: *Alphitobius*). The basal metabolic rate of the predator individuals were measured in O_2-chambers of an automated electrolytic microrespirometer (Scheu 1992). Measurements were replicated at six temperatures (5, 10, 15, 20, 25 and 30 °C) for each of the three predators (five replicates per predator*temperature combination). The measurements ran for 24 hours, the last three hours were averaged to result in the basal metabolic rate, and the O_2 fluxes (ml O_2/h) were

transferred into energetic equivalents (J/h) by letting 1 ml O_2 = 20.1 J (Peters 1983).

Each experimental unit included one predator individual and prey at different initial densities (6 replicates per density) varying between low densities (1, 3, 5, 10, 20, 30 prey individuals per experimental arena) and higher prey densities that were adjusted to each specific predator-prey combination to reach saturation in the predators *per capita* consumption rate (e.g., 120 individuals of *Drosophila* for *Calathus fuscipes* and 200 individuals of *Drosophila* for *Harpalus rufipes* at 30°C). The predator individuals were deprived of food for one week prior to the start of the experiments that were carried out in Perspex® arenas (20x20x10 cm equaling 400 cm^2) covered with lids that had holes to allow gas exchange. The ground was covered with moist dental cast (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.43 g dry weight) that was first dried for several days at 40°C to exclude other animals and then re–moisturized. Prey individuals were placed in the arenas half an hour in advance of the predators to allow them to adjust to the arenas. The experiments were run for 24 h with a day/night rhythm of 12/12 h dark/light. Initial and final prey densities were used to calculate the number of prey eaten. Control experiments without predators showed that prey mortality or escape did not influence our experiments.

Statistical Analyses

To account for prey depletion (decreasing N during the time course of the experiments) we used Rogers's random predator equation (Rogers 1972):

$$N_e = N\left[1-\exp\left(aN\left(h N_e - T_t\right)\right)\right] \qquad (2.4.3)$$

where N_e is the number of prey eaten, T_t is the total experimental time, and N is the initial prey density. We fitted equ. (3) to the data using Newton's method (Juliano et al. 2001) while preventing negative handling times. Fitting of more complex type-III functional response models (Vucic-Pestic et al. 2010) yielded non-significant trends in attack rates with prey density, which rendered their application unnecessary.

Our experiments resulted in 90 measurements of basal metabolic rates I [J/s] (five for each combination of predator and temperature), and 18 independent estimates of attack rates a [0.04 m²/h] and handling time h [h/Ind] for each for of the two prey species (three predators across six temperatures). Based on metabolic theory (Brown et al. 2004) these variables should depend on the body masses, M [g] and the environmental temperature, T [K]:

$$I = I_0 M^{b_I} e^{\frac{E_I T_0 - T}{kTT_0}} \qquad (2.4.4a)$$

$$h = h_0 M^{b_h} e^{\frac{E_h T_0 - T}{kTT_0}} \quad (2.4.4b)$$

$$a = a_0 M^{b_a} e^{\frac{E_a T_0 - T}{kTT_0}} \quad (2.4.4c)$$

where I_0, h_0 and a_0 are intercepts at temperature T_0 of 17.5°C (= 290.65 K) equal to the mean of our experimental temperature gradient (5° - 30°C), b_I, b_h *and* b_a are allometric exponents, E_I, E_h and E_a are activation energies, k is Boltzmann's constant (Vasseur and McCann 2005). After linearising these equations by natural logarithms, we used linear, least-squares regressions for parameter estimation.

After converting average weights [g] of prey individuals (Table 2.4.1) into their average energy content [J] (1 kg wet mass = 7x 10^6 Joule; Peters 1983), we calculated dimensionless ingestion efficiencies, y, of the predators by dividing ingestion, F, by metabolism, I:

$$y = \frac{F}{I} \quad (2.4.5)$$

By inserting the mass- and temperature-dependence models of handling time and attack rate (equ. 5, 6) in the ingestion model (equ. 1), and subsequently inserting the ingestion model (equ. 1) and the respiration model (equ. 4) in equ. (7), we obtained a model of ingestion efficiencies depending on predator mass and environmental temperature. Additionally, F depends on prey abundance, N, which can be predicted by:

$$N = N_0 M^{b_K} e^{\frac{E_K}{kT}} \sigma^z e^{tl_0(tl-1)} \quad (2.4.6)$$

where N_0 is a normalization constant, b_K, z and tl_0 are constants, E_K is the activation energy, σ is the annual net primary productivity of the habitat [g(C) m^{-2} y^{-1}], and tl is the trophic level (Allen et al. 2005; Meehan 2006a) For soil animals these constants are: $N_0 = e^{-31.15}$, b_K = -0.72, E_K = 0.71, tl_0 = -2.86, z = 1.03 and tl = 1.5 for decomposers, fungivores and herbivores (Meehan 2006a). The net primary productivity in equ. (8) equals:

$$\sigma = \sigma_0 e^{\frac{E\sigma T_0 - T}{kTT_0}} \quad (2.4.7)$$

where σ_0 is the net primary productivity at temperature T_0 [K] and E_σ is the activation energy (Allen et al. 2005). We assumed a net primary production, σ_0, of 600 g(C) $m^{-2}y^{-1}$ for temperate regions (Cramer et al. 1999) at a T_0 of 9.5°C (282.65 K), which equals the average annual temperature in Germany (Deutscher Wetterdienst 2007).

d) Results

We tested for significant trends in predator metabolic rates, handling times and attack rates depending on predator body mass and environmental temperature. For the three predator species of our study, we found significant increases in metabolism with predator mass (Figure 2.4.1a) and temperature (Figure 2.4.1b). Subsequently, the functional response model (equ. 2.4.3) was fitted separately to the ingestion data for each combination of predator-prey interaction and temperature, which yielded substantial variance in handling times ($0.37 \leq T_h \leq 18.24$ [h/ind]) and attack rates ($0.002 \leq b \leq 0.84$ [0.04m²/h]) (see Appendix for data). Our analyses show significant decreases in handling time with increasing predator mass (Figure 2.4.1c) and warming (Figure 2.4.1d) for both prey species. Interestingly, the activation energies of handling time were much lower (*Alphitobius*: 0.23; *Drosophila*: 0.24, Figure 2.4.1d) than the activation energy of metabolism (0.61, Figure 2.4.1b). The attack rates of the predators on the mobile prey, *Drosophila*, decreased with predator body mass and increased with warming, whereas the attack rates of the same predators on the resident prey, *Alphitobius*, were influenced neither by predator body mass nor by environmental temperature (Figure 2.4.1e, f).

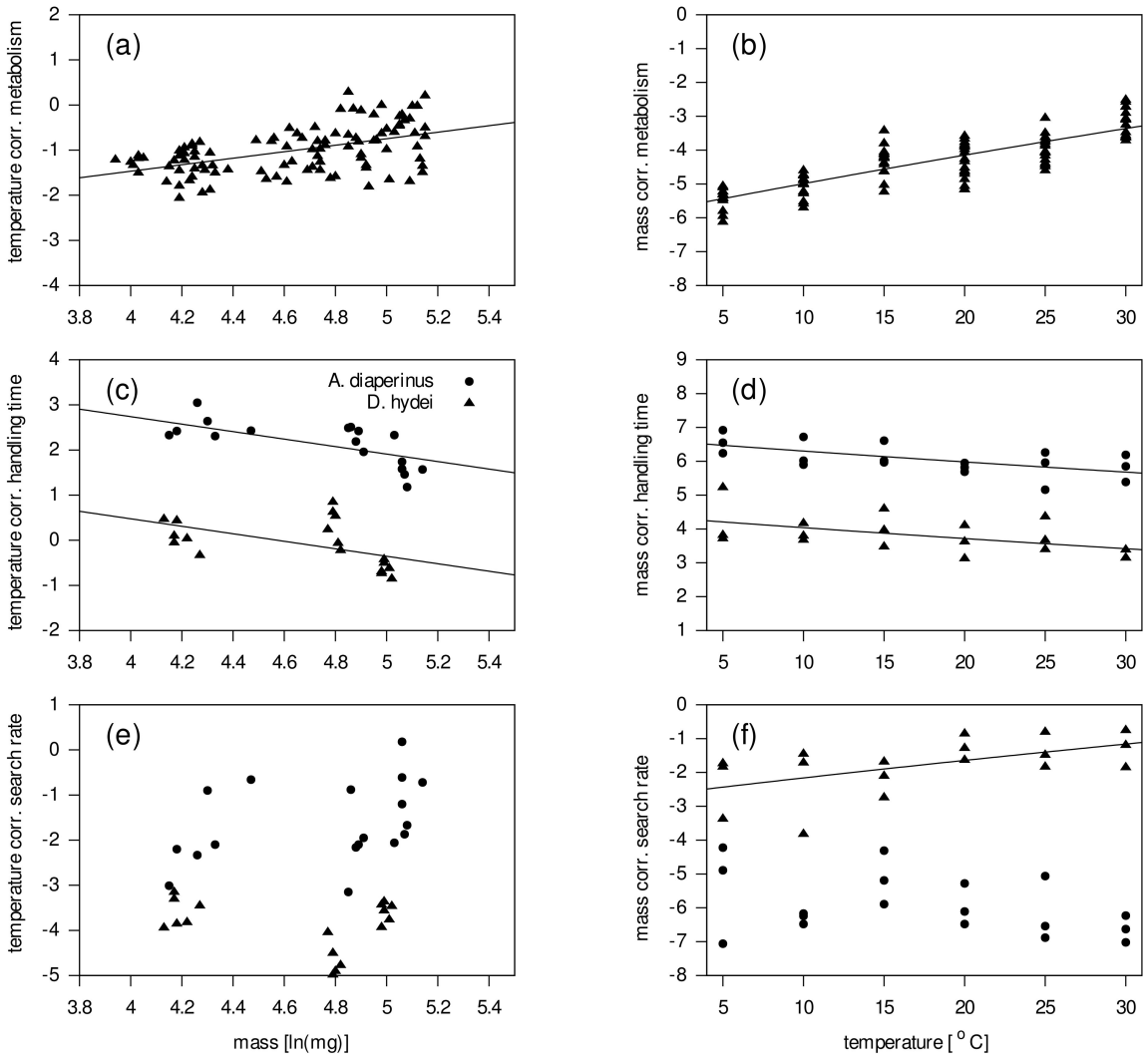

Figure 2.4.1: Predator metabolism *I* (a, b), handling time *h* (c, d) and search rate *a* (e, f) depending on predator body mass [mg] (a, c, e) and the environmental temperature [°C] (b, d, f). Data are ln-transformed and the dependent variables are normalized by their temperature dependence (a, c, e) or their body mass dependence (b, d, f). Temperature axes are untransformed. Regression model parameters (and standard errors in brackets) for (a, b) metabolism (equation 3): I_0 = -3.91 (0.59), b_I = 0.62 (0.13), E_I = -0.61 (0.04), r^2 = 0.75, $p < 0.001$, n = 90; (c, d) handling time (equation 4): *Alphitobius* h_0 = 6.85 (1.18), b_h = -0.99 (0.25), E_h = 0.23 (0.07), r^2= 0.63, $p < 0.001$, n = 18; *Drosophila* h_0= 2.99 (1.57), b_h = -0.66 (0.34), E_h = 0.24 (0.1), r^2 = 0.4, $p < 0.05$, n = 18; (e, f) attack rate (equation 5): *Alphitobius* a_0 = -5.94 (2.83), b_a = 0.91 (0.59), E_a = 0.27 (0.18), r^2 = 0.24, p = 0.13, n = 18; *Drosophila* a_0= -1.77 (2.33), b_a = -0.48 (0.5), E_a = -0.37 (0.15), r^2 = 0.33, $p < 0.05$, n = 18.

The fitted regression models of handling time and attack rates depending on predator body mass and environmental temperature (Figure 2.4.1) can be inserted in the functional response model (equ. 2.4.3). The resulting synthetic functional response model predicts the *per capita* ingestion rates of the predators depending on predator body-mass, environmental temperature and prey density (Figure 2.4.2). Across all predator-prey combinations in our study, the *per capita* ingestion rates were well described by the synthetic model except for slight underestimations of the largest predators (*Pterostichus melanarius*) at the highest prey densities (Figure 2.4.2e, f).

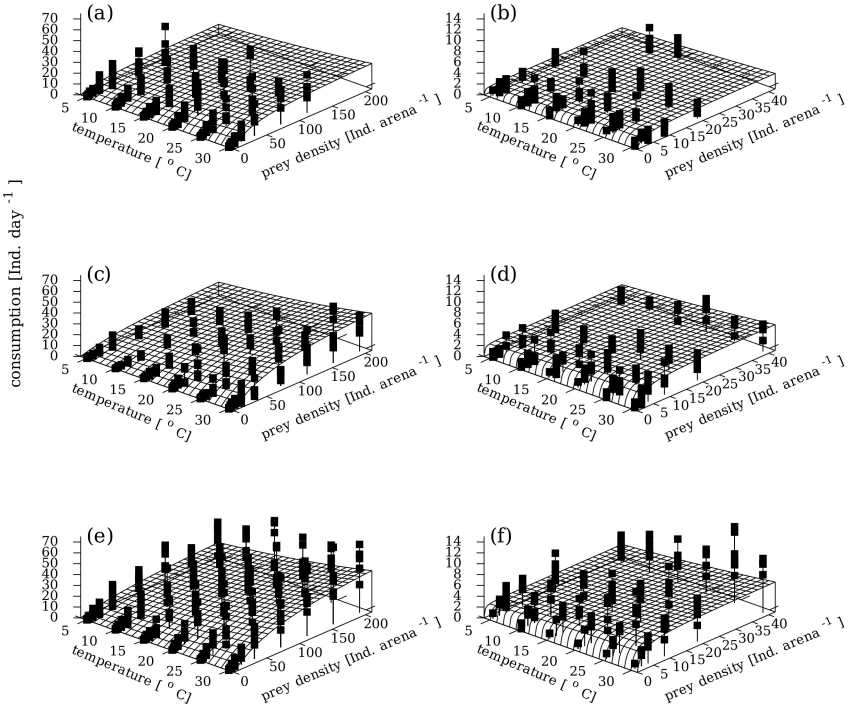

Figure 2.4.2: Experimental *per capita* ingestion rates depending on environmental temperature [°C] and prey density (*N*). The planes show the predictions of the synthetic functional response model based on the allometric and temperature scaling relationships in Fig. 1 for a) C. fuscipes/Drosophila, b) *C. fuscipes*/*Alphitobius*, c) *H. rufipes*/ *Drosophila*, d) *H. rufipes*/*Alphitobius* and e) *P. melanarius*/*Drosophila*, f) *P. melanarius*/*Alphitobius*.

Accounting for the trends in the *per capita* rates of ingestion and metabolism yields decreases in ingestion efficiencies with increasing temperature (Figure 2.4.3). While ingestion rates exceeded the metabolic loss rates roughly ten- to thirtyfold at the lowest experimental temperaturs of 5° Celsius, we found much lower ratios (one- to eightfold) at the highest temperature of 30° Celsius. In addition, the ingestion efficiencies increased and decreased with predator body mass when preying on *Alphitobius* (Figure 2.4.3a) and *Drosophila* (Figure 2.4.3b), respectively. This pattern is consistent with similar trends in attack rates (Figure 2.4.1).

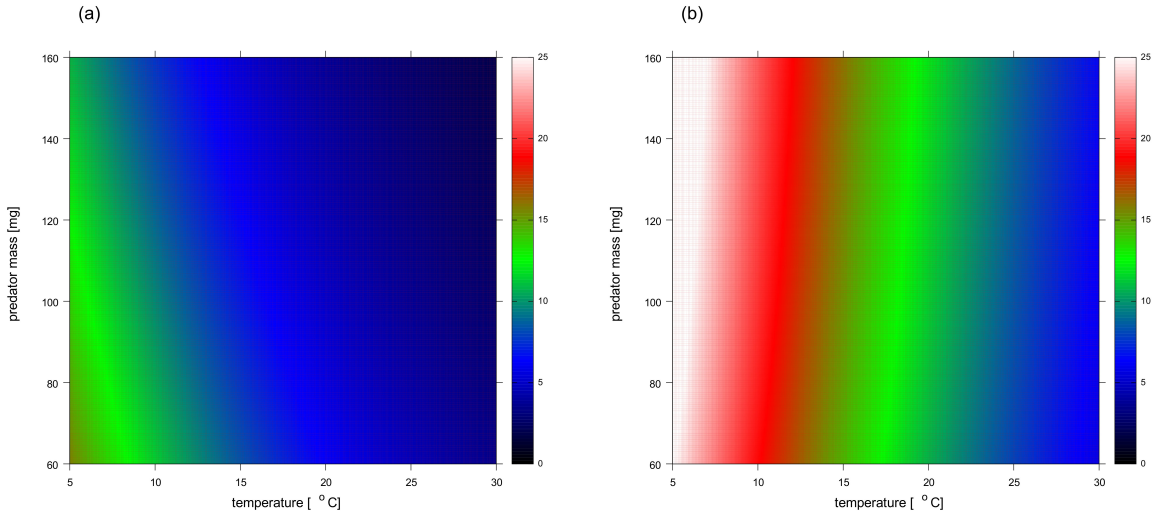

Figure 2.4.3: Predator ingestion efficiency y_{ij} in treatments with *Alphitobius* as prey (a) and *Drosophila* as prey (b). On the x-axis are the predator masses [mg] and on the y-axis the temperature [°C].

e) Discussion

This study shows that the metabolic rates and functional responses of three common terrestrial predators of different body masses on one mobile and one resident prey depended on environmental temperature in ways that were consistent with expectations. Corroborating metabolic theory (Brown et al. 2004; Meehan 2006b), we found exponential and power-law increases in metabolism with increasing temperature and body mass, respectively. The decreases in handling time with increasing temperature and body mass support the findings of prior studies with different species (Bailey 1989; Bergman 1987; Cave and Gaylor 1989; Dreisig 1981; Garcia-Martin et al. 2008; Gilioli et al. 2005; Gresens et al. 1982; McCoull et al. 1998; Song and Heong 1997; Thompson 1978; Xia et al. 2003; Zhang et al. 1999, 1998), which indicates the broad generality of these scaling relationships. However, these prior studies documented a plethora of temperature scaling models for attack rates. Consistent with our initial concept, we demonstrate for the first time to our knowledge that attack rates increase with warming when predators feed on mobile prey, whereas they are independent of environmental temperature if the same predators feed on resident prey.

We suggest the following explanation for the different warming effects on attack rates. The net effect of warming on attack rates depends on the ratio between the twofold positive effect on encounter rates via increased predator and prey mobility and the simple negative effect via prey escape efficiency. Accordingly, the two-fold positive effect on encounter rates with mobile prey such as *Drosophila* in our experiments should outweigh the negative effect on prey escape efficiencies to result in a positive net effect of warming on attack rates. In

contrast, warming did not increase the mobility of the resident prey, *Alphitobius*, in our experiment, and the positive effect of warming on predator mobility was counteracted by the negative effect on via increased prey escape efficiency, which prevented a warming effect on attack rates. Behavioural observations during the experiments support this interpretation: *Alphitobius* individuals did not increase their movement, but they twitched more strongly under increased temperature, which led to more unsuccessful attacks.

This study contributes toward general understanding of warming effects on predator-prey interaction strengths by presenting a concept that differentiates between metabolically driven effects on handling time and behavioural effects on attack rates. As for any laboratory study, some caveats have to be mentioned: we did not take into account more complex aspects of interactions such as prey switching behaviour, interference competition or thermal adaptation. In addition, we did not address warming effects on functional responses including resident predators (e.g., sessile filter feeders) or resources without escape efficiencies (e.g., detritus). While logistic constraints prevented these additional experiments in the present study, we are confident that the concept of warming effects on attack rates outlined here is of broad generality.

Our results provide strong evidence that warming imposes energetic restrictions on predators by decreasing their ingestion efficiencies (i.e., the ratio of ingestion and metabolism). In consequence, warming should increase population stability with less fluctuations in population densities over time (Rall et al. 2008; Vasseur and McCann 2005). Consistent with a prior study of linear interaction strengths (Rall et al. 2010), our results also suggest that decreasing ingestion efficiencies impose the risk of predator starvation on natural ecosystems, which may explain severe consumer extinctions in warmed microcosms (Petchey et al. 1999). Eventually, the mechanistic functional-response framework of the present study may allow detailed predictions on the consequences of warming on predator-prey interaction strengths depending on metabolic and behavioural constraints.

Table 2.4.1: Estimates of *Th* [h/ind] and *b* [0.04m²/h]. *Th* = handling time, *b* = attack rate, Temperature is shown in °C and mass in mg.

predator	temp [°C]	mass [mg]	N	*Th*	SE	*attack*	SE	R^2
D. hydei (1.91mg)								
C. fuscipes	5	65.02	48	1.44	0.17	0.022	0.000	0.40
C. fuscipes	10	64.69	61	1.41	0.15	0.025	0.003	0.65
C. fuscipes	15	62.01	58	1.73	0.21	0.017	0.002	0.52
C. fuscipes	20	71.81	54	0.66	0.06	0.036	0.003	0.57
C. fuscipes	25	65.65	56	1.23	0.11	0.031	0.004	0.52
C. fuscipes	30	67.79	48	0.71	0.06	0.041	0.004	0.79
H. rufipes	5	119.93	55	3.54	0.86	0.004	0.001	0.33
H. rufipes	10	122.77	54	1.21	0.61	0.002	0.000	0.51
H. rufipes	15	121.82	55	1.87	0.37	0.007	0.001	0.63
H. rufipes	20	117.57	55	1.17	0.11	0.020	0.003	0.52
H. rufipes	25	120.68	55	1.49	0.15	0.016	0.002	0.40
H. rufipes	30	124.53	64	0.55	0.07	0.016	0.002	0.64
P. melanarius	5	151.23	63	0.65	0.07	0.016	0.002	0.68
P. melanarius	10	145.70	67	0.64	0.06	0.022	0.002	0.74
P. melanarius	15	145.91	65	0.52	0.06	0.017	0.002	0.57
P. melanarius	20	147.23	62	0.61	0.04	0.039	0.004	0.68
P. melanarius	25	146.61	66	0.48	0.03	0.042	0.004	0.77
P. melanarius	30	150.53	65	0.37	0.02	0.043	0.003	0.76
A.diaperinus (23.26mg)								
C. fuscipes	5	87.17	33	17.28	2.69	0.84	1.43	0.09
C. fuscipes	10	63.60	40	13.21	2.62	0.07	0.04	0.14
C. fuscipes	15	65.11	36	12.25	1.99	0.12	0.08	0.17
C. fuscipes	20	75.59	32	9.34	2.29	0.11	0.09	0.28
C. fuscipes	25	73.44	32	11.05	1.78	0.31	0.33	0.2

C. fuscipes	30	70.82	31	14.32	3.71	0.06	0.05	0.23
H. rufipes	5	127.74	37	18.24	3.96	0.07	0.06	0.1
H. rufipes	10	132.74	36	14.37	2.34	0.16	0.11	0.08
H. rufipes	15	129.10	49	13.29	1.79	0.46	0.61	0.09
H. rufipes	20	135.64	37	6.58	0.95	0.13	0.06	0.47
H. rufipes	25	152.30	37	8.12	1.18	0.1	0.04	0.32
H. rufipes	30	131.36	34	6.07	0.92	0.07	0.02	0.42
P. melanarius	5	169.97	36	0.83	0.79	0.79	0.85	0.34
P. melanarius	10	158.98	42	0.54	0.21	0.21	0.07	0.48
P. melanarius	15	158.02	36	0.58	1.31	1.31	2.01	0.47
P. melanarius	20	157.97	36	0.45	0.5	0.5	0.3	0.6
P. melanarius	25	161.11	40	0.24	0.14	0.14	0.03	0.71
P. melanarius	30	157.88	39	0.33	0.19	0.19	0.06	0.77

2.5. Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction

a) Abstract

Functional responses describe the *per capita* consumption rates of predators depending on prey density, which quantifies the energy transfer between trophic levels. We studied a typical interaction of the litter-soil systems between hunting spiders (*Pardosa lugubris*; Araneae: Lycosidae) and springtails (*Heteromurus nitidus*; Collembola: Entomobryidae) at varying habitat structure, i.e. with moss versus without moss. We found a hyperbolic increase in consumption (functional response type II) in the treatment without habitat structure that was converted into a roller-coaster (or dome-shaped in a broad sense) functional response in treatments with habitat structure. Additional experiments suggest that the reduced *per capita* consumption rates at high prey densities may be explained by aggregative defence behaviour of Collembola. Experimentally, this behaviour was induced by the presence of habitat structure. We analyzed the net-energy gain of this predator-prey interaction by comparing the predator's metabolic energy loss to its energy gain by consumption. In treatments with habitat structure, the net-energy gain of the predator was limited at intermediate prey densities where prey aggregation reduced the consumption rates. Our results stress the importance of habitat structure and prey behaviour in shaping the functional response in a typical soil-litter predator-prey interaction. As human activity directly alters habitat structure in forest systems, our findings may have profound implications for population dynamics and food-web structure in soil-litter systems.

b) Introduction

Functional responses quantify the per capita consumption rates of predators depending on prey abundance. They are thus of central importance for understanding predator-prey and community dynamics in natural ecosystems (Brose, Jonsson, et al. 2006; Oaten and Murdoch 1975; Rall et al. 2008; Williams and Martinez 2004). The increase in consumption rates with prey abundance can be linear up to a constant plateau (type I), hyperbolic (type II), sigmoid (type III), dome-shaped (type IV) or roller-coaster shaped (Jeschke and Tollrian 2005a). Generally, the most basic type of a functional response is described by Holling's type II model with the parameters search rate (i.e., instantaneous rate of successful search, sometimes referred to as attack rate) and handling time (Holling 1959a). All other functional response types can be deduced from it (Jeschke et al. 2004). If the handling time of the predator is negligible, as it is often assumed for filter feeders, the type II response reduces to a type I

functional response. If search rates increase with prey density, the type II functional response is converted into a type III functional response. This can be the case if a predator exploits the prey more effectively at high prey densities (Real 1979), switches between different resources depending on their relative densities (Elliott 2004; Murdoch 1969), or changes its foraging tactics. For instance, search rates may increase with prey density when refuges, e.g. due to habitat structure, offer shelter for only a limited number of prey individuals (Scheffer and De Boer 1995). If the search rates or their success decrease at high prey densities, the type II (or type III) functional response is converted into a type IV (dome-shaped) functional response (Jeschke and Tollrian 2005a). This dome-shaped functional response characterizes predator-prey interactions when the number of consumed prey individuals first increases and then decreases with increasing prey density. For instance, successful attacks at high prey densities may decrease when prey has active or inducible defence behaviour such as aggregation or swarming that is induced by the predator at high prey densities (Jeschke 2006, 2007; Jeschke and Tollrian 2005a). Interestingly, the functional response can also become roller-coaster shaped when predator consumption rates decrease at intermediate prey densities (as for dome-shaped functional responses) and subsequently increase again at high prey densities (Jeschke and Tollrian 2005a).

Here, we present a study on the functional response in a predator-prey interaction between wolf spiders and Collembola, which commonly occur in the litter layer of temperate forests. We hypothesized that the complex habitat structure of the litter layer affects the shape of the functional response. Without habitat structure we expected a type II functional response with constant search rates, whereas with habitat structure we expected that spatial refuges for the prey population result in more complex functional responses with search rates that depend on prey density (type III, dome-shaped or roller-coaster shaped). Subsequently, we compare the energetic expenditure of the predator in terms of its basal metabolic rate to the energy gain by foraging.

c) Materials and Methods

The predator in our experiment was the wolf spider *Pardosa lugubris* Walckenaer (Araneae: Lycosidae), which is a widespread polyphageous consumer that dominates many forest litter communities in central Europe. Wolf spiders are non web-building predators which are mainly optically oriented. They hunt for prey with a sit-and-pursue strategy characterized by changes in foraging sites (Nyffeler et al. 1994). We used the Collembola species *Heteromurus nitidus* Templeton (Entomobryidae) as prey in our experiment. *Heteromurus nitidus* occurs in the litter layer of temperate forests and colonizes the upper soil layer for breeding. The individuals in our experiments were taken from laboratory cultures.

Functional response experiments

In a first experiment, we tested the influence of habitat structure on the functional response in our predator-prey interaction by establishing two different treatments with moss as habitat structure (structure treatment) or without moss (no-structure treatment). In both treatments, one spider was added as a predator and adult Collembola were supplied in densities of 1, 3, 5, 8, 12, 18, 26, 36, 100 and 300 individuals. In both treatments, we set up six replicates per prey density resulting in a total of 60 experimental units per treatment.

Adult female spiders were collected in the Kranichstein forest near Darmstadt (Hesse, Germany) one day prior to the experiments. They were kept separately in plastic jars, sprayed with water and were deprived of food for 24 h before the start of the experiment. Each spider individual was used only once. The experiments were performed in round plastic jars, 8.2 cm in diameter and 4.5 cm high. An amount of 1.42 g dry moss (*Polytrichum formosum*) was added to the jars of the replicates with habitat structure. The moss was collected from the same site as the spiders, and it was dried for five days in a drying chamber at 80°C to exclude other animals from the experiment. Water was added by a disperser to keep the experimental containers moist. *Heteromurus* individuals were placed in the plastic jars 0.5 h before the spider to allow them to adjust to the arenas. The experiment was run for 24 h under greenhouse conditions (natural photoperiod) at 18°C during the day and 16°C at night. At the end of the experiment, we counted the number of surviving Collembola.

To account for prey depletion during the experiment we used a generalized model of Rogers's random predator equation (Rogers 1972) for parameter fitting.

$$N_e = N_0\left(1 - e^{a(N_e T_h - PT)}\right) \qquad (2.5.1)$$

where P is the number of predators, N_e is the number of prey eaten, N_0 is the initial prey density, a is the search rate, T_h is the handling time, and T is the total time of the experiment. We solved this recursive function of N_e with a maximum likelihood method using the packages "bblme" and "emdbook" provided by the statistical software package "R" (Bolker 2008; R Development Core Team 2008).

Equ. (1) describes type II functional responses, whereas functional responses with prey-density dependent search rates, a, require more complex models with additional parameters:

$$a = \frac{e^{\varepsilon(\varphi - N_0)}}{1 + e^{(1+\beta)\varepsilon(\varphi - N_0)}}\left(\varepsilon_{\max} - \varepsilon_{\min}\right) + \varepsilon_{\min} \qquad (2.5.2)$$

describing a hump-shaped curve varying the search rate, a, between a maximum (ε_{max}) and a minimum (ε_{min}) with the shape parameters β for the increasing part of the hump, ε for the

decreasing part of the hump, and φ is a half saturation constant (see Jeschke & Tollrian, 2005 and Bolker, 2008 for details).

Aggregation experiment

We studied the aggregation behaviour of Collembola depending on habitat structure (with moss vs. without moss) under predator presence with 10 replicates per treatment resulting in a total of 20 replicates. Adult female spiders were collected one day prior to the experiment and kept under equal conditions as in the functional response experiment. The experiment was conducted in rectangular plastic boxes, 10 cm long, 6 cm wide and 2.3 cm high. We measured aggregation by drawing a grid with 15 cells (2 x 2 cm) on the lid and counting the number of individuals in each cell (x_1, x_2, …, x_{15}) after letting the Collembola adjust for half an hour. Subsequently, we calculated the Morisita Index of Dispersion I_δ (Krebs 1989):

$$I_\delta = n\,[(\sum x^2 - \sum x)/((\sum x)^2 - \sum x)] \qquad (2.5.3)$$

where n is the sample size, $\sum x$ is the sum of prey in quadrate counts ($x_1 + x_2 + \ldots + x_{15}$) and $\sum x^2$ is the sum of prey in quadrate counts squared ($x_1^2 + x_2^2 + \ldots + x_{15}^2$). Then we calculated two critical values for the Morisita Index:

$$M_U = \frac{\chi^2_{0.975} - n + \sum x_i}{\left(\sum x_i\right) - 1} \qquad (2.5.4a)$$

$$M_C = \frac{\chi^2_{0.025} - n + \sum x_i}{\left(\sum x_i\right) - 1} \qquad (2.5.4b)$$

where M_U is the uniform index, M_C is the clumped index, $\chi^2_{0..975}$ and $\chi^2_{0.025}$ are the values of chi-squared with n-1 degrees of freedom that have 97.5% and 2.5% of the area to the right, respectively. We calculated the standardized Morisita Index I_p by:

if $I_\delta \geq M_c > 1.0$ $\qquad I_p = 0.5 + 0.5\left(\frac{I_d - M_C}{n - M}\right)$ (2.5.5a)

if $M_c > I_\delta \geq 1.0$ $\qquad I_p = 0.5\left(\frac{I_d - 1}{M_U - 1}\right)$ (2.5.5b)

if $1.0 > I_\delta > M_u$ $\qquad I_p = -0.5\left(\frac{I_d - 1}{M_U - 1}\right)$ (2.5.5c)

if $1.0 > M_u > I_\delta$ $\qquad I_p = -0.5 + 0.5\left(\frac{I_d - M_U}{M_U}\right)$ (2.5.5d)

The standardized Morisita Index of dispersion I_p ranges from -1.0 to +1.0. Random patterns result in an I_p of zero, aggregated patterns have above zero and uniform patterns below zero values (Krebs 1989). Spiders on average consumed 2-3 Collembola in treatments without moss which changed the total number of individuals in these replicates. This small error was not corrected for when calculating the Morisita Index. In treatments with moss, it was not possible to count all individuals, because some of them were hidden under the moss. A reduction in *n* in these treatments would have led to a distortion of the results compared to other treatments. Accordingly, we did not account for a reduction in *n* by spider consumption or hidden prey during the experiment and used the initial *n* throughout all replicates. We used an ANOVA to test for the effect of the fixed factor habitat structure on the aggregation of the Collembola (the standardized Morisita Index of Dispersion).

Metabolic rates

The basal metabolic rates of fourteen individuals of *P. lugubris* were measured as O_2 consumption. The measurements lasted for 24 h, and the final three hours were averaged to calculate the basal metabolic rate. The measurements were carried out in small chambers (3 cm diameter) using an automated electrolytic microrespirometer measuring O_2 consumption (Scheu 1992). We transformed the measured O_2 fluxes (ml O_2 h^{-1}) per spider individual into energetic equivalents (J h^{-1}) by assuming 1 ml O_2 = 20.1 J (Peters 1983). To determine the energy gain due to consumption we weighed ten individuals of *H. nitidus* in six replicates and calculated the mean weight of one Collembola individual. Then, we calculated the average energy content of Collembola individuals by using the conversion equation: 1 kg wet mass = 7 x 10^6 J (Peters 1983). This allowed comparing the energy expenditure of individual spiders in terms of their metabolic rates per day to their energy gain by consumption during our functional response experiments.

d) Results

Functional response

The density of Collembola prey and the addition of moss as habitat structure significantly affected the *per capita* consumption rate of *P. lugubris*. In the treatment without moss, the consumption rate was generally higher than in the treatment with moss, except for the lowest prey density (Figure 2.5.1a, b). In the treatment without moss, consumption increased hyperbolically indicating a type II functional response (Figure 2.5.1a). The estimated search rate, a = 0.133 ± 0.008 (mean ± SE) and handling time, T_h = 0.25 ± 0.01 (mean ± SE) were highly significant ($p<0.001$, $r^2= 0.87$). In the treatment with moss, the *per capita* consumption rate first increased, then decreased and rose again with prey density, which characterizes a

roller-coaster functional response (Figure 2.5.11b). To obtain accurate parameter estimates for this functional response, we calculated search rates according to equ. 2.5.1 based on the assumption that handling time is not affected by habitat structure (i.e., we used the same handling time as estimated for the treatment without moss in Figure 2.5.1a). Subsequently, we fitted equ. 2.5.2 to the data to describe the dependency of search rates on prey density (Figure 2.5.1c). While the decrease of the hump (ε), the maximum search rate (ε_{max}) and the half-saturation constant (φ) were significant, the increase (β) and the minimum search rate (ε_{min}) were lacking significance (Fig. 1c).

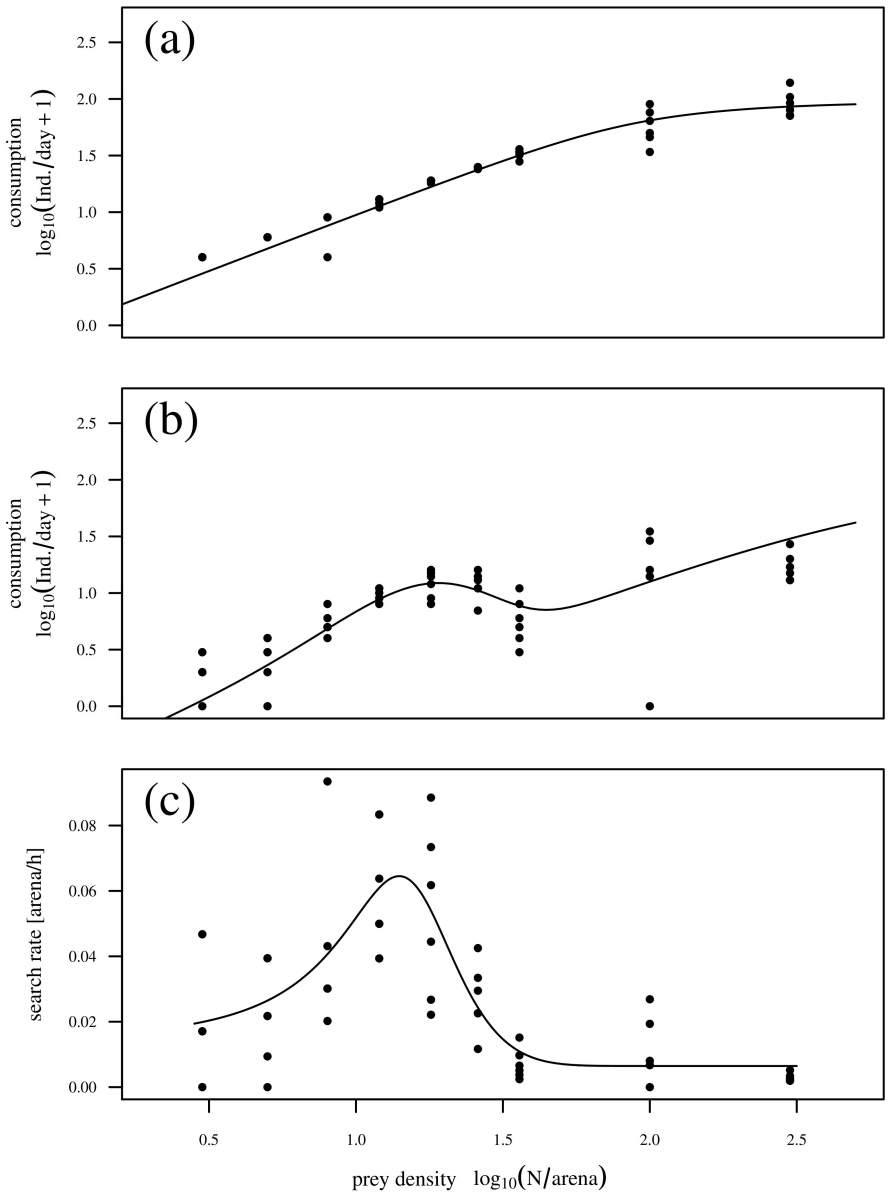

Figure 2.5.1: *Per capita* comsumption rate of the spider *Pardosa lugubris* dependinng on the number of individuals of the Collembila prey *Heteromurus nitidus* in a) treatments without habitat structure and b) with moss as habitat structure. c) Search rate of the predator *P. lugubris* in dependence on prey density (r^2=0.58). Curve fitting by equ 2.5.2, ε=0.14 ± 0.06 ($p<0.01$), φ=12.83 ± 2.87 ($p<0.001$), β=1.53 ± 1.05 (n.s.), ε_{min}=0.006 ±0.004 (n.s.) and ε_{max}=0.12±0.01 ($p<0.001$)

Aggregation

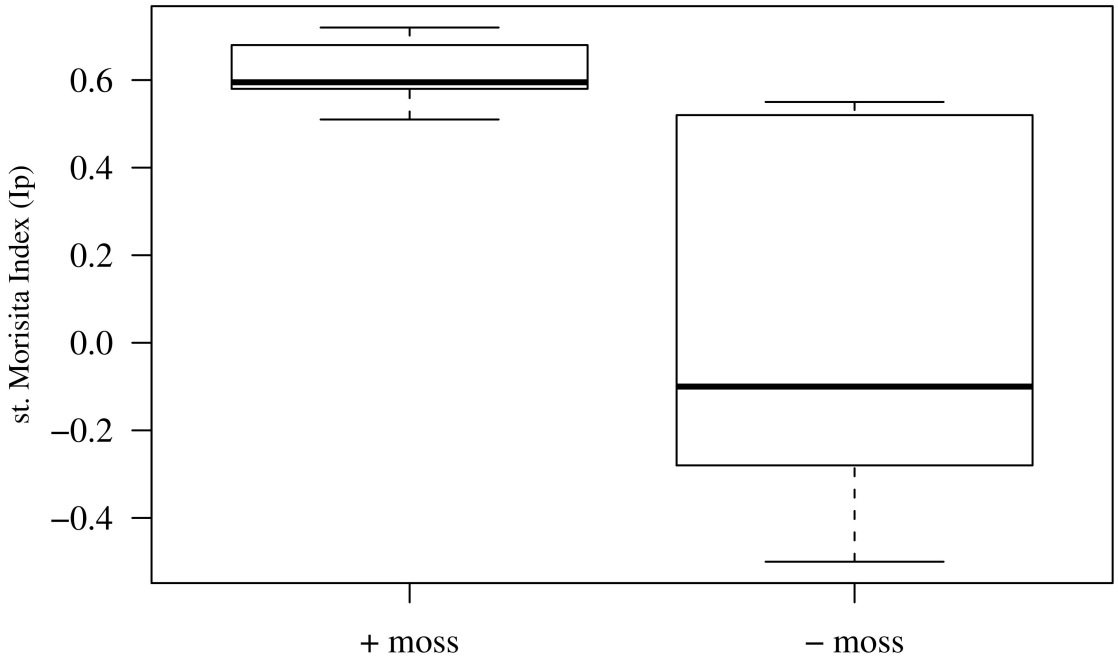

Figure 2.5.2: Collembola aggregation (mean and standard error of the Morisita Index of Dispersion) in treatments with moss 0.62±0.13 (mean± SE, p<0.001, GLM) and without moss 0.05±0.09 mean±

We studied the aggregation of the Collembola with spider presence in dependence on moss as habitat structure. In treatments with moss, the Collembola showed an aggregated distribution (i.e., Morisita index significantly higher than zero), whereas the distribution was random in treatments without moss (Morisita index not significantly different from zero, Figure 2.5.2).

Metabolic rates

The basal metabolic rate of wolf spiders in our experiment was 3.73 ± 0.92 J d^{-1} (mean ± standard deviation, n = 14). Subsequently, we compared these metabolic expenses to the energy gain by consumption of Collembola in our functional response experiments with and without moss as habitat structure (Figure 2.5.3). In the treatment with moss, the energy uptake at prey densities up to 12 individuals per arena was lower than the basal energetic expense. At intermediate prey densities (12-26 individuals), the energy gain (ca. 6-8 J d^{-1}; Figure 2.5.3) was higher than the basal energetic expense. For instance, at a prey density of 18 individuals, the *per capita* consumption rate of the spider was 2.18 times the basal metabolic rate in the treatment with moss (8.15 J d^{-1}), while at higher prey densities (36-50 individuals) the energy gain was again lower and more similar to the basal energetic expense. At Collembola densities higher than 50 individuals per arena the energy gain increased continuously to exceed the basal energetic expense.

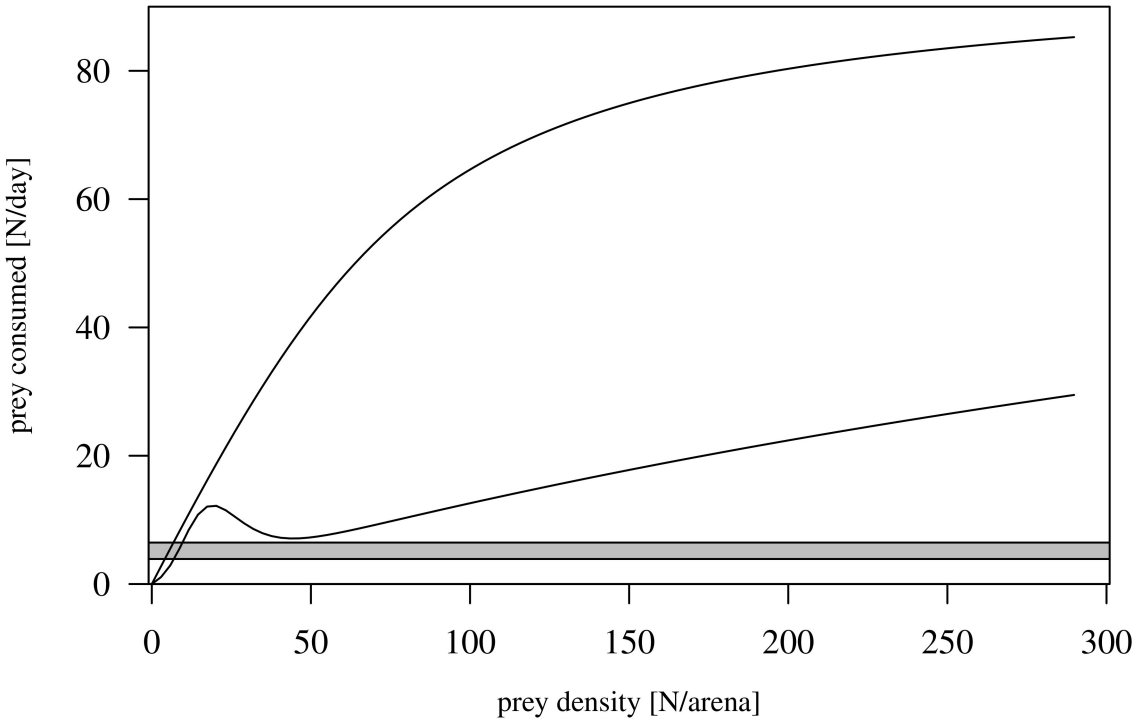

Figure 2.5.3: Energetic constraints on Pardosa lugubris preying on Heteromurus nitidus dependending on prey density. Per capita energy loss to the basal metabolic rate (solid grey line show the standard deviation of the basal metabolic rate, energetic expense [J d-1] is converted into individuals of H. nitidus) and per capita consumption of Collembola individuals (functional responses).

e) Discussion

Results of our study on the functional response of the wolf spider *P. lugubris* feeding on the Collembola *H. nitidus* suggest that (1) habitat structure may change a type II into a roller-coaster functional response (or dome-shaped in a broad sensu Jeschke & Tollrian 2005), (2) the presence of habitat structure may lead to aggregation of the Collembola, and (3) habitat structure influences the energetic profitability of an interaction (energy gain by consumption relative to energy loss by basal respiration). Together, these results confirm that habitat structure and prey aggregation have profound implications for predator-prey interaction strengths.

Prior studies on spider functional responses without habitat structure suggested a type I functional response (Provencher and Coderre 1987). In contrast, we found a type II functional response in treatments without habitat structure. This disparity might be explained by the fact that prey densities in prior experiments may have been too low to observe saturation in the consumption rate, which hampers proper fits of functional response models (Jeschke et al. 2004). Generally, habitat structure may provide refuges for prey which reduces the success of

the search rates of predators at low prey densities (Birkhofer et al. 2008; Rickers and Scheu 2005), which should lead to sigmoid type III functional responses. While we found increases in search rates at low prey densities (see Figure 2.5.1c) indicating sigmoid functional responses, these increases were not significant in the fitted hump-shaped model (parameter β in equ. 2.5.2, see Figure 2.5.1c). Interestingly, our results suggest that the presence of habitat structure yields significant decreases in the success of the search rates at higher prey densities (parameter ε in equ. 2.5.2, see Figure 2.5.1c). These decreases indicate dome-shaped (minimum successful search rate of zero at high prey densities) or roller-coaster shaped functional responses (successful search rate significantly higher than zero; Jeschke & Tollrian, 2005). While our results demonstrate that the *per capita* consumption rates increase at high prey density – consistent with a roller-coaster shaped functional response – our analyses of search rates documented minimum search rates that were not statistically different from zero indicating a dome-shaped functional response. As the latter result is explained by the general difficulty in obtaining significance for a non-linear, multi-parameter model, we conclude that habitat structure can induce a roller-coaster shaped (or dome-shaped in a broad sense sensu Jeschke & Tollrian, 2005) functional response when the prey has defensive strategies such as aggregation that are related to habitat structure.

Consistent with our interpretation of the results, decreasing consumption rates at higher prey densities in prior studies have been explained by prey defence or swarming effects (Crawley 1992; Negri 2004). Our results extend these findings to predator-prey interactions in terrestrial soil systems, where the aggregation behaviour of the Collembola that we documented in treatments with habitat structure may be responsible for the roller-coaster functional response that we found in the same treatments. This finding may be of broad generality across other predator-prey interactions involving Collembola prey that generally use aggregation pheromones (Nilsson and Bengtsson 2004). This suggests that complex functional response models involving density-dependent prey defences (Jeschke et al. 2006; Jeschke 2006, 2007; Jeschke and Tollrian 2005a) may be of broad generality in soil ecosystems.

In the presence of a predator, aggregation is advantageous for Collembola individuals because it reduces foraging success due to early warning by conspecifics, risk spreading amongst the individuals in the cluster and predator confusion (Young et al. 1994). Aggregation may therefore act as a cooperative predator defence mechanism: if a predator captures one prey individual from the swarm (i.e. the cluster), other individuals may be able to escape. Thus, the larger a group is the lower is the predation risk for every prey individual within the group. However, *per capita* consumption rates of the functional response in our study rose again at very high prey densities. A possible explanation could be that at these prey densities high encounter rates outweighed the defence benefits of aggregation.

As a consequence of the roller-coaster functional response in the treatments with moss the

basal metabolic rate of *P. lugubris* exceeded the *per capita* consumption rates below prey densities of 12 and resembled the *per capita* consumption rates between densities of 36-50 individuals per arena. Our results suggest that feeding on *H. nitidus* leads to a net energy gain by the spiders only at specific ranges of Collembola densities. The range of Collembola densities with net energy gain for the predator might be even narrower if the field metabolic rate is considered, which is often higher than the basal metabolic rate (Savage, Gillooly, Woodruff, et al. 2004). The maximal metabolic rates during the first two hours of our experiments when the spiders were stressed by laboratory handling were approximately two to three times higher than the basal metabolic rates (data not shown). The field metabolic rate ranges between the basal and the maximum metabolic rate (Savage, Gillooly, Brown, et al. 2004), and we speculate that it should be closer to the basal metabolic rate, because the spiders are sit-and-pursue predators that do not always move under natural conditions (Samu et al. 2003).

In terrestrial systems habitat structure influences micro-climate conditions leading to patchy, aggregated distributions of predator and prey populations according to their environmental demands (Materna 2004; Poole 1962; Rypstra et al. 2007). In addition to this dominant effect of habitat structure on species distributions, our results stress the importance of habitat structure for predator-prey interactions. Increases in habitat complexity decrease not only the encounter rate by offering refuges (Real 1977), they can also induce aggregation behaviour of the prey leading to dome-shaped or roller-coaster shaped functional responses. Interestingly, our results also suggest that these effects of habitat structure on the shape of the functional response determine energetic efficiencies of the predator-prey interactions. These findings indicate important links between habitat structure and the energetic functionality of terrestrial soil ecosystems.

3. Bibliography

Abrahams MV, Mangel M, Hedges K (2007) Predator-prey interactions and changing environments: who benefits? Philosophical Transactions of the Royal Society B-Biological Sciences 362: 2095-2104.

Abrams PA (1990) The effects of adaptive behavior on the type-2 functional response. Ecology 71: 877–885.

Akre BG, Johnson DM (1979) Switching and sigmoid functional response curves by damselfly naiads with alternative prey available. The Journal of Animal Ecology: 703–720.

Aljetlawi AA, Sparrevik E, Leonardsson K (2004) Prey-predator size-dependent functional response: derivation and rescaling to the real world. Journal of Animal Ecology 73: 239-252.

Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. Science 297: 1545-1548. doi:10.1126/science.1072380

Allen AP, Gillooly JF, Brown JH (2005) Linking the global carbon cycle to individual metabolism. Ecology 19: 202–213.

Allen CR, Garmestani AS, Havlicek TD, Marquet PA, Peterson GD, Restrepo C, Stow CA, Weeks BE (2006) Patterns in body mass distributions: sifting among alternative hypotheses. Ecology Letters 9: 630-643.

Bailey PCE (1989) The effect of water temperature on the functional response of the water stick insect Ranatra dispar (Heteroptera: Nepidae). Austral Ecology 14: 381-386. doi:10.1111/j.1442-9993.1989.tb01448.x

Bascompte J, Melián C, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America 102: 5447, 5443.

Bascompte J, Melian CJ (2005) Simple trophic modules for complex food webs. Ecology 86: 2868-2873.

Baulch H, Schindler D, Turner M, Findlay D, Paterson M, Vinebrooke R (2005) Effects of warming on benthic communities in a boreal lakelake: Implications of climate change. Limnology and Oceanography 50: 1377-1392.

Beckerman AP, Petchey OL, Warren PH (2006) Foraging biology predicts food web complexity. Proceedings of the National Academy of Sciences 103: 13745-13749.

Beddington JR, Hassell MP, Lawton JH (1976) The components of arthropod predation: II. The predator rate of increase. The Journal of Animal Ecology: 165–185.

Belovsky GE (1997) Optimal foraging and community structure: The allometry of herbivore food selection and competition. Evolutionary Ecology 11: 641-672. doi:10.1023/A:1018430201230

Bergman E (1987) Temperature-dependent differences in foraging ability of two percids, Perca fluviatilis and Gymnocephalus cernuus. Environmental Biology of Fishes 19: 45–53.

Berlow EL (1999) Strong effects of weak interactions in ecological communities. Nature 398: 330-334.

Berlow EL, Brose U, Martinez ND (2008) The “Goldilocks factor” in food webs. Proceedings of the National Academy of Sciences 105: 4079-4080.

Berlow EL, Neutel AM, Cohen JE, de Ruiter PC, Ebenman BO, Emmerson M, Fox JW, Jansen VAA, Jones JI, Kokkoris GD (2004) Interaction strengths in food webs: issues and opportunities. Ecology 73: 585-598.

Berlow EL, Dunne JA, Martinez ND, Stark PB, Williams RJ, Brose U (2009) Simple prediction of interaction strengths in complex food webs. Proceedings of the National Academy of Sciences 106: 187-191. doi:10.1073/pnas.0806823106

Berlow EL, Navarrete SA, Briggs C, Power ME, Menge B (1999) Quantifying variation in the strengths of species interactions. Ecology 80: 2206–2224.

Bersier LF, Banašek-Richter C, Cattin MF (2002) Quantitative descriptors of food-web matrices. Ecology 83: 2394-2407. doi:10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2

Bersier L, Kehrli P (2008) The signature of phylogenetic constraints on food-web structure. Ecological Complexity 5: 132-139. doi:10.1016/j.ecocom.2007.06.013

Birkhofer K, Wise DH, Scheu S (2008) Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. Oikos 117: 494.

Bjorkman C, Liman AS (2005) Foraging behaviour influences the outcome of predator-predator interactions. Ecological Entomology 30: 164–169.

Bolker BM (2008) Ecological models and data in R. Princeton Univ Pr

Brose U (2008) Complex food webs prevent competitive exclusion among producer species. Proceedings of the Royal Society B: Biological Sciences 275: 2507-2514. doi:10.1098/rspb.2008.0718

Brose U, Berlow EL, Martinez ND (2005) Scaling up keystone effects from simple to complex ecological networks. Ecology Letters 8: 1317-1325.

Brose U, Ehnes RB, Rall BC, Vucic-Pestic O, Berlow EL, Scheu S (2008) Foraging theory predicts predator-prey energy fluxes. Journal of Animal Ecology 77: 1072–1078.

Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier LF, Blanchard JL, Brey T, Carpenter SR (2006) Consumer–resource Body-Size Relationships in Natural Food Webs. Ecology 87: 2411-2417. doi:10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2

Brose U, Williams RJ, Martinez ND (2006) Allometric scaling enhances stability in complex food webs. Ecology Letters 9: 1228-1236.

Brose U Body-mass constraints on foraging behaviour determine population and food-web dynamics. Functional Ecology. doi:10.1111/j.1365-2435.2009.01618.x

Brown JH, Gillooly JF (2003) Ecological food webs: High-quality data facilitate theoretical unification. Proceedings of the National Academy of Sciences of the United States of America 100: 1467-1468. doi:10.1073/pnas.0630310100

Brown J, Gillooly J, Allen A, Savage V, West G (2004) Toward a metabolic theory of ecology. Ecology 85: 1771–1789.

Bystrom P, Persson L, Wahlstrom E, Westman E (2003) Size-and density-dependent habitat use in predators: consequences for habitat shifts in young fish. Journal of Animal Ecology 72: 156-168.

Carbone C, Mace GM, Roberts SC, Macdonald DW (1999) Energetic constraints on the diet of terrestrial carnivores. Nature 402: 286-288.

Carbone C, Teacher A, Rowcliffe JM (2007) The costs of carnivory. PLoS Biology 5: 363–368.

Cattin MF, Bersier LF, Banasek-Richter C, Baltensperger R, Gabriel JP (2004) Phylogenetic constraints and adaptation explain food-web structure. Nature 427: 835-839.

Cave RD, Gaylor MJ (1989) Functional response of Telenomus reynoldsi [Hym.: Scelionidae] at five constant temperatures and in an artificial plant arena. BioControl 34: 3–10.

Charnov EL (1976) Optimal foraging: attack strategy of a mantid. The American Naturalist 110: 141.

Chen X, Xu X, Ji X (2003) Influence of body temperature on food assimilation and locomotor performance in white-striped grass lizards, Takydromus wolteri (Lacertidae). Journal of Thermal Biology 28: 385-391. doi:10.1016/S0306-4565(03)00022-6

Clark DB, Castro CS, Alvarado LDA, Read JM (2004) Quantifying mortality of tropical rain forest trees using high-spatial-resolution satellite data. Ecology Letters 7: 52-59. doi:doi:10.1046/j.1461-0248.2003.00547.x

Clarke A (2004) Is there a universal temperature dependence of metabolism? Functional Ecology 18: 252-256.

Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. Journal of Animal Ecology 68: 893–905.

Cohen JE, Pimm SL, Yodzis P, Saldaña J (1993) Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62: 67-78.

Cowie RJ (1977) Optimal foraging in great tits (Parus major). Nature 268: 137-139. doi:10.1038/268137a0

Cramer W, Kicklighter DW, Bondeau A, Moore B, Churkina G, Nemry B, Ruimy A, Schloss AL, others (1999) Comparing global models of terrestrial net primary productivity(NPP): overview and key results. Global Change Biology 5: 1–15.

Crawley MJ (1992) Natural Enemies: The Population Biology of Predators, Parasites and Diseases. Oxford Blackwell Scientific Publication

Crowl TA, Covich AP (1990) Predator-induced life-history shifts in a freshwater snail. Science 247: 949.

Daufresne M, Boet P (2007) Climate change impacts on structure and diversity of fish communities in rivers. Global Change Biology 13: 2467-2478. doi:10.1111/j.1365-

2486.2007.01449.x

Dawidowicz P, Loose CJ (1992) Metabolic costs during predator-induced diel vertical migration of Daphnia. Limnology and Oceanography: 1589–1595.

De Angelis DL (1975) Stability and connectance in food web models. Ecology 56: 238-243.

De Angelis DL, Holland JN (2006) Emergence of ratio-dependent and predator-dependent functional responses for pollination mutualism and seed parasitism. Ecological modelling 191: 551–556.

Deutscher Wetterdienst (2007) Klimastatusbericht 2007. Deutscher Wetterdienst. http://www.dwd.de/bvbw/generator/Sites/DWDWWW/Content/Oeffentlichkeit/KU/KU2/KU22/klimastatusbericht/einzelne__berichte/download__ksb2007,templateId=raw,property=publicationFile.pdf/download_ksb2007.pdf

Dreisig H (1981) The rate of predation and its temperature dependence in a tiger beetle, Cicindela hybrida. Oikos 36: 196–202.

Dunne JA, Williams RJ, Martinez ND (2002) Food-web structure and network theory: The role of connectance and size. Proceedings of the National Academy of Sciences of the United States of America 99: 12917-12922.

von Elert E, Loose CJ (1996) Predator-induced diel vertical migration inDaphnia: Enrichment and preliminary chemical characterization of a kairomone exuded by fish. Journal of Chemical Ecology 22: 885–895.

Elliott JM (2003) Interspecific interference and the functional response of four species of carnivorous stoneflies. Freshwater Biology 48: 1527–1539.

Elliott JM (2004) Prey switching in four species of carnivorous stoneflies. Freshwater Biology 49: 709-720.

Emmerson M, Yearsley JM (2004) Weak interactions, omnivory and emergent food-web properties. Proceedings of the Royal Society B - Biological Sciences 271: 397-405.

Emmerson MC, Montoya JM, Woodward G (2005) Body size, interaction strength, and food web dynamics. In: Dynamic Food Webs: Multispecies assemblages, ecosystem development, and environmental change. Academic Press, pp. 167-178

Emmerson MC, Raffaelli D (2004) Predator-prey body size, interaction strength and the stability of a real food web. Journal of Animal Ecology 73: 399-409. doi:10.1111/j.0021-8790.2004.00818.x

Finstad AG, Ugedal O, Berg OK (2006) Growing large in a low grade environment: size dependent foraging gain and niche shifts to cannibalism in Arctic char. Oikos 112: 73-82. doi:10.1111/j.0030-1299.2006.13990.x

Foelix RF (1996) Biology of Spiders. Oxford University Press

Forchhammer MC, Post E (2000) Climatic signatures in ecology. Trends in Ecology & Evolution 15: 286. doi:10.1016/S0169-5347(00)01869-3

Fussmann GF, Blasius B (2005) Community response to enrichment is highly sensitive to model structure. Biology Letters 1: 9-12. doi:10.1098

Garcia-Martin M, Gamez M, Torres-Ruiz A, Cabello T (2008) Functional response of Chelonus oculator (Hymenoptera : Braconidae) to temperature, and its consequences to parasitism. COMMUNITY ECOLOGY 9: 45-51. doi:10.1556/ComEc.9.2008.1.6

Gentleman WC, Neuheimer AB (2008) Functional responses and ecosystem dynamics: how clearance rates explain the influence of satiation, food-limitation and acclimation. Journal of Plankton Research 30: 1215-1231.

Gergs A, Ratte HT (2009) Predicting functional response and size selectivity of juvenile Notonecta maculata foraging on Daphnia magna. Ecological Modelling: 3331-3341.

Gilioli G, Baumgartner J, Vacante V (2005) Temperature influences on functional response of Coenosia attenuata (Diptera : Muscidae) individuals. Journal of Economic Entomology 98: 1524-1530.

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of Size and Temperature on Metabolic Rate. Science 293: 2248-2251. doi:10.1126/science.1061967

Ginzburg L, Akcakaya H (1992) Consequences of ratio-dependent predation for steady-state properties of ecosystems. Ecology 73: 1536-1543.

Gresens SE, Cothran ML, Thorp JH (1982) The influence of temperature on the functional response of the dragonfly Celithemis fasciata (Odonata: Libellulidae). Oecologia 53: 281-284. doi:10.1007/BF00388999

Hairston J, Hairston S (1997) Does food web complexity eliminate trophic-level dynamics? The American Naturalist 149: 1001-1007.

Hassell MP (1978) The Dynamics of Arthropod Predator-Prey Systems. Princeton University Press

Hassell MP, Lawton JH, Beddington JR (1976) The components of arthropod predation: I. The prey death-rate. Journal of Animal Ecology 45: 135–164.

Hassell MP, Lawton JH, Beddington JR (1977) Sigmoid functional responses by invertebrate predators and parasitoids. Journal of Animal Ecology 46: 249-262.

Hassell MP, Lawton JH, May RM (1976) Patterns of dynamical behaviour in single-species populations. Journal of Animal Ecology 45: 471-486.

Hassell MP, May RM (1973) Stability in insect host-parasite models. Journal of Animal Ecology 42: 693-726.

Holling CS (1959a) Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91: 385-398.

Holling CS (1959b) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist: 293-319.

Holt R, Polis G (1997) A theoretical framework for intraguild predation. American Naturalist 149: 745-764.

Hughes L (2002) Biological consequences of global warming. Climate Change: Critical Concepts in the Environment 5: 283.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15: 56-61.

Jeschke J (2006) Density-dependent effects of prey defenses and predator offenses. Journal of Theoretical Biology 242: 900-907.

Jeschke J (2007) When carnivores are "full and lazy". Oecologia 152: 357-364.

Jeschke J, Kopp M, Tollrian R (2006) Time and energy constraints: reply to Nolet and Klaassen (2005). Oikos 114: 553-554.

Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. Ecological Monographs 72: 95–112.

Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79: 337–349.

Jeschke JM, Tollrian R (2005a) Effects of predator confusion on functional responses. Oikos 111: 547–555.

Jeschke JM, Tollrian R (2005b) Predicting herbivore feeding times. Ethology 111: 187-206.

Jeschke JM, Kopp M, Tollrian R (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. Biological Reviews 79: 337-349. doi:10.1017/S1464793103006286

Juliano SA, Scheiner SM, Gurevitch J (2001) Design and Analysis of Ecological Experiments. In: Design and analysis of ecological experiments. Oxford University Press, NY, pp. 178-198

Kareiva P, Mullen A, Southwood R (1990) Population dynamics in spatially complex environments: theory and data [and discussion]. Philosophical Transactions: Biological Sciences 330: 175–190.

Kingsolver J, Woods H (1997) Thermal sensitivity of growth and feeding in Manduca sexta caterpillars. Physiological Zoology 70: 631-638.

Kingsolver JG, Woods HA (1998) Interactions of temperature and dietary protein concentration in growth and feeding of Manduca sexta caterpillars. Physiological Entomology 23: 354–359.

Koen-Alonso M (2007) A Process-Oriented Approach to the Multispecies Functional Response. In: From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems. Springer Netherlands, pp. 1-36. http://dx.doi.org/10.1007/978-1-4020-5337-5_1. Accessed 6 Feb 2009

Kondoh M (2003) Foraging Adaptation and the Relationship Between Food-Web Complexity and Stability. Science: 1388-1391.

Kozlowski J, Konarzewski M (2004) Is West, Brown and Enquist's model of allometric scaling mathematically correct and biologically relevant? Functional Ecology 18: 283-289.

Kratina P, Vos M, Bateman A, Anholt BR (2009) Functional responses modified by predator

density. Oecologia 159: 425-433. doi:10.1007/s00442-008-1225-5

Krebs CJ (1989) Ecological methodology. Harper & Row New York

Krebs J (1977) Optimal foraging: theory and experiment. Nature 268: 583-584. doi:10.1038/268583a0

Kusch J (1993) Predator-induced morphological changes in Euplotes (Ciliata): Isolation of the inducing substance released from Stenostomum sphagnetorum (Turbellaria). Journal of Experimental Zoology 265: 613–613.

Lawton J (1970) Feeding and food energy assimilation in larvae of damselfly Pyrrhosoma nymphula (Sulz) (Odonata - Zygoptera). Journal of Animal Ecology 39: 669-689.

Lenski R, Benett A (1993) Evolutionary response of Escherichia coli to thermal-stress. American Naturalist 142: 47-64.

Lima SL (1998) Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48: 25–34.

Loeuille N, Loreau M (2005) Evolutionary emergence of size-structured food webs. Proceedings of the National Academy of Sciences 102: 5761.

Makarieva A, Gorshkov V, Li B (2005) Energetics of the smallest: do bacteria breathe at the same rate as whales? Proceedings of the Royal Society B - Biological Sciences 272: 2219-2224.

Mann ME (2007) Climate over the past two millennia. Annual Review of Earth and Planetary Sciences: 111-136. doi:10.1146/annurev.earth.35.031306.140042

Mann ME, Bradley RS, Hughes MK (1998) Northern hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. Geophysical Research Letters 26:

759–762.

Martinez ND (1992) Constant connectance in community food webs. The American Naturalist 139: 1208–1218.

Materna J (2004) Does forest type and vegetation patchiness influence horizontal distribution of soil Collembola in two neighbouring forest sites? Pedobiologia-International Journal of Soil Biology 48: 339–347.

May RM (1972) Will a large complex system be stable. Nature 238: 413-414.

May RM (1973) Stability and Complexity in Model Ecosystems / Population Biology Monographs No. 6. Princeton University Press

McAllister CD, Lebrasseur RJ, Parsons TR, Rosenzweig ML (1972) Stability of enriched aquatic ecosystems. Science 175: 562-565. doi:10.1126/science.175.4021.562

McArdle BH, Lawton JH (1979) Effects of prey-size and predator-instar on the predation of Daphnia by Notonecta. Ecological entomology 4: 267–275.

McCann KS, Hastings A, Huxel GR (1998) Weak trophic interactions and the balance of nature. Nature 395: 794-798.

McCann K (2000) The diversity-stability debate. Nature 405: 228-233.

McConnachie S, Alexander G (2004) The effect of temperature on digestive and assimilation efficiency, gut passage time and appetite in an ambush foraging lizard, Cordylus melanotus melanotus. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 174: 99-105. doi:10.1007/s00360-003-0393-1

McCoull CJ, Swain R, Barnes RW (1998) Effect of temperature on the functional response and components of attack rate in Naucoris congrex St\aal (Hemiptera: Naucoridae). Australian

Journal of Entomology 37: 323–327.

Meehan TD (2006a) Mass and temperature dependence of metabolic rate in litter and soil invertebrates. Physiological and Biochemical Zoology 79: 878–884.

Meehan TD (2006b) Energy use and animal abundance in litter and soil communities. Ecology 87: 1650–1658.

Meer JVD (2006) Metabolic theories in ecology. Trends in Ecology & Evolution 21: 136-140. doi:10.1016/j.tree.2005.11.004

Mills NJ (1982) Satiation and the functional response: a test of a new model. Ecological Entomology 7: 305–315.

Montoya JM, Pimm SL, Solé RV (2006) Ecological networks and their fragility. Nature 442: 259-264.

Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39: 335-354.

Murdoch WW, Oaten A (1975) Predation and population stability. Advances in Ecological Research 9: 1-131.

Murdoch WW (1975) Switching, functional response, and stability in predator-prey systems. American Naturalist 109: 299-318.

Nakamura K (1974) A model of the functional response of a predator to prey density involving the hunger effect. Oecologia 16: 265–278.

Navarrete SA, Berlow EL (2006) Variable interaction strengths stabilize marine community pattern. Ecology Letters 9: 526-536.

Negri I (2004) Spatial distribution of Collembola in presence and absence of a predator. Pedobiologia 48: 585-588. doi:10.1016/j.pedobi.2004.07.004

Neutel A, Heesterbeek JAP, de Ruiter PC (2002) Stability in real food webs: Weak links in long loops. Science 296: 1120-1123.

Neutel A, Heesterbeek JAP, van de Koppel J, Hoenderboom G, Vos A, Kaldeway C, Berendse F, de Ruiter PC (2007) Reconciling complexity with stability in naturally assembling food webs. Nature 449: 599-602. doi:10.1038/nature06154

Nilsson E, Bengtsson G (2004) Death odour changes movement pattern of a Collembola. Oikos 104: 509–517.

Norberg RA (1988) Theory of growth geometry of plants and self-thinning of plant populations: geometric similarity, elastic similarity, and different growth modes of plant parts. American Naturalist 131: 220–256.

Nyffeler M, Sterling WL, Dean DA (1994) How spiders make a living. Environmental entomology 23: 1357–1367.

Oaten A, Murdoch W (1975) Switching, functional response, and stability in predator-prey systems. American Naturalist 109: 299-318.

O'Gorman EJ, Emmerson MC (2009) Perturbations to trophic interactions and the stability of complex food webs. Proceedings of the National Academy of Sciences 106: 13393.

Otto S, Berlow E, Rank N, Smiley J, Brose U (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web(vol 89, pg 134, 2008). Ecology 89: 888-888.

Otto SB, Rall BC, Brose U (2007) Allometric degree distributions facilitate food-web stability. Nature 450: 1226-1230.

Paine RT (1966) Food Web Complexity and Species Diversity. The American Naturalist 100: 65-75.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Reviews in Ecology and Systematics: 637-669. doi:10.1146/annurev.ecolsys.37.091305.110100

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13: 1860-1872. doi:10.1111/j.1365-2486.2007.01404.x

Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. Bulletin of the American Meteorological Society 81: 443-450.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579-583.

Peckarsky B, Abrams P, Bolnick D, Dill L, Grabowski J, Luttbeg B, Orrock J, Peacor S, Preisser E, Schmitz O, Trussell G (2008) Revisiting the classics: Considering nonconsumptive effects in textbook examples of predator-prey interactions. ECOLOGY 89: 2416-2425.

Persson L (1985) Asymmetrical competition: are larger animals competitively superior? The American Naturalist 126: 261–266.

Persson L, Leonardsson K, de Roos AM, Gyllenberg M, Christensen B (1998) Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. Theoretical Population Biology 54: 270–293.

Petchey OL, Beckerman AP, Riede JO, Warren PH (2008) From the Cover: Size, foraging, and food web structure. Proceedings of the National Academy of Sciences 105: 4191-4196.

Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. Nature 402: 69-72. doi:10.1038/47023

Peters RH (1983) The Ecological Implications of Body Size. Cambridge University Press

Poole TB (1962) The effect of some environmental factors on the pattern of distribution of soil Collembola in a coniferous woodland. Pedobiologia 2: 169–182.

Provencher L, Coderre D (1987) Functional responses and switching of Tetragnatha laboriosa Hentz (Araneae: Tetragnathidae) and Clubiona pikei Gertsh (Araneae: Clubionidae) for the aphids Rhopalosiphum maidis (Fitch) and Rhopalosiphum padi (L.)(Homoptera: Aphididae). Environmental Entomology 16: 1305–1309.

Rall BC, Guill C, Brose U (2008) Food-web connectance and predator interference dampen the paradox of enrichment. Oikos 117: 202-213.

Rall BC, Vucic-Pestic O, Ehnes RB, Emmerson MC, Brose U (2010) Temperature, predator-prey interaction strength and population stability. Global Change Biology. doi:10.1111/j.1365-2486.2009.02124.x

R Development Core Team (2008) R: A Language and Environment for Statistical Computing. Vienna, Austria. http://www.R-project.org

R Development Core Team (2009) R: A Language and Environment for Statistical Computing. Vienna, Austria. http://www.R-project.org

Real L (1977) Kinetics of functional response. American Naturalist 111: 289-300.

Real LA (1979) Ecological determinants of functional response. Ecology 60: 481-485.

Reuman DC, Cohen JE (2005) Estimating relative energy fluxes using the food web, species abundance, and body size. Advances in Ecological Research 36: 137-182.

Rickers S (2005) Regulation of wolf spider populations. Universitäts-und Landesbibliothek

Darmstadt

Rickers S, Scheu S (2005) Cannibalism in Pardosa palustris (Araneae, Lycosidae): effects of alternative prey, habitat structure, and density. Basic and Applied Ecology 6: 471-478. doi:10.1016/j.baae.2005.02.007

van Rijn PCJ, Bakker FM, Hoeven WADVD, Sabelis MW (2005) Is arthropod predation exclusively satiation-driven? Oikos 109: 101-116. doi:doi:10.1111/j.0030-1299.2005.12987.x

Rogers D (1972) Random search and insect population models. Journal of Animal Ecology 41: 369-383.

Rosenberg AA, Bolster WJ, Alexander KE, Leavenworth WB, Cooper AB, McKenzie MG (2005) The history of ocean resources: modeling cod biomass using historical records. Frontiers in Ecology and the Environment 3: 78–84.

Roughgarden J (1975) A simple model for population dynamics in stochastic environments. American Naturalist: 713–736.

de Ruiter P, Neutel A, Moore J (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269: 1257-1260.

Rypstra AL, Schmidt JM, Reif BD, DeVito J, Persons MH (2007) Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. Oikos 116: 853–863.

Samu F, Szirányi A, Kiss B (2003) Foraging in agricultural fields: local `sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. Animal Behaviour 66: 939-947. doi:10.1006/anbe.2003.2265

Sanford E (1999) Regulation of keystone predation by small changes in ocean temperature. Science 283: 2095-2097.

Sarnelle O, Wilson A (2008) Type III functional response in Daphnia. Ecology 89: 1723-1732.

Savage VM, Gillooly JF, Brown JH, West GB, Charnov EL (2004) Effects of Body Size and Temperature on Population Growth. The American Naturalist 163: 429-441. doi:10.1086/381872

Savage VM, Gillooly JF, Woodruff WH, West GB, Allen AP, Enquist BJ, Brown JH (2004) The predominance of quarter-power scaling in biology. Functional Ecology 18: 257-282.

Scheffer M, De Boer RJ (1995) Implications of spatial heterogeneity for the paradox of enrichment. Ecology 76: 2270-2277.

Schenk D, Bacher S (2002) Functional response of a generalist insect predator to one of its prey species in the field. Journal of Animal Ecology 71: 524–531.

Schenk D, Bersier LF, Bacher S (2005) An experimental test of the nature of predation: neither prey-nor ratio-dependent. Ecology 74: 86-91. doi:10.1111/j.1365-2656.2004.00900.x

Scheu S (1992) Automated Measurement of the Respiratory Response of Soil Microcompartments - Active Microbial Biomass in Earthworm Feces. Soil Biology & Biochemistry 24: 1113-1118.

Schmitz OJ (2007) Predator diversity and trophic interactions. Ecology 88: 2415–2426.

Schoener TW (1983) Rate of species turnover decreases from lower to higher organisms: a review of the data. Oikos: 372–377.

Skalski GT, Gilliam JF (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. Ecology 82: 3083-3092. doi:10.1890/0012-9658

Smith FE (1963) Population dynamics in Daphnia magna and a new model for population growth. Ecology 44: 651–663.

Smout S, Lindstroem U (2007) Multispecies functional response of the minke whale Balaenoptera acutorostrata based on small-scale foraging studies. Marine Ecology Progress Series 341: 277-291.

Solomon ME (1949) The natural control of animal populations. Journal of Animal Ecology 18: 1-35.

Solow AR, Beet AR (1998) On lumping species in food webs. Ecology 79: 2013–2018.

Song YH, Heong KL (1997) Changes in searching responses with temperature ofCyrtorhinus lividipennis Reuter (Hemiptera: Miridae) on the eggs of the brown planthopper, Nilaparvata lugens (Stal.)(Homoptera: Delphacidae). Researches on Population Ecology 39: 201–206.

Spitze K (1992) Predator-mediated plasticity of prey life history and morphology: Chaoborus americanus predation on Daphnia pulex. The American Naturalist 139: 229–247.

Spitze K (1985) Functional response of an ambush predator: Chaoborus americanus predation on Daphnia pulex. Ecology(Durham) 66: 938-949.

Stemberger RS (1988) Reproductive costs and hydrodynamic benefits of chemically induced defenses in Keratella testudo. Limnology and Oceanography 33: 593–606.

Stenson JA (1987) Variation in capsule size of Holopedium gibberum (Zaddach): a response to invertebrate predation. Ecology 68: 928–934.

Stephens DW, Charnov EL (1982) Optimal foraging: Some simple stochastic models. Behavioral Ecology and Sociobiology 10: 251-263. doi:10.1007/BF00302814

Stouffer DB, Camacho J, Amaral LAN (2006) A robust measure of food web intervality. Proceedings of the National Academy of Sciences of the United States of America 103: 19015-19020.

Thompson DJ (1978) Towards a Realistic Predator-Prey Model: The Effect of Temperature on the Functional Response and Life History of Larvae of the Damselfly, Ischnura elegans. The Journal of Animal Ecology 47: 757-767. doi:10.2307/3669

Thompson DJ (1975) Towards a predator-prey model incorporating age structure - effects of daphnia-magna by ischnura-elegans. Journal of Animal Ecology 44: 907-916.

Tollrian R (1995) Predator-induced morphological defenses: costs, life history shifts, and maternal effects in Daphnia pulex. Ecology 76: 1691–1705.

Troost T, Kooi B, Dieckmann U (2008) Joint evolution of predator body size and prey-size preference. Evolutionary Ecology 22: 771-799. doi:10.1007/s10682-007-9209-1

Uchida S, Drossel B, Brose U (2007) The structure of food webs with adaptive behaviour. Ecological Modelling 206: 263-276. doi:10.1016/j.ecolmodel.2007.03.035

Vance-Chalcraft H, Rosenheim J, Vonesh J, Osenberg C, Sih A (2007) The influence of intraguild predation on prey suppression and prey release: A meta-analysis. Ecology 88: 2689-2696.

Vance-Chalcraft HD, Soluk DA (2005) Multiple predator effects result in risk reduction for prey across multiple prey densities. Oecologia 144: 472–480.

Vasseur DA, McCann KS (2005) A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. The American Naturalist 166: 184–198.

Vonesh JR, Bolker BM (2005) Compensatory larval responses shift trade-offs associated with predator-induced hatching plasticity. Ecology 86: 1580–1591.

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. Journal of Animal Ecology 79: 249–256. doi:10.1111/j.1365-2656.2009.01622.x

Wahlström E, Persson L, Diehl S, Byström P (2000) Size-dependent foraging efficiency, cannibalism and zooplankton community structure. Oecologia 123: 138-148

Walther G (2007) Tackling Ecological Complexity in Climate Impact Research. SCIENCE-NEW YORK THEN WASHINGTON- 5812: 606.

Weitz JS, Levin SA (2006) Size and scaling of predator-prey dynamics. Ecology Letters 9: 548-557. doi:10.1111/j.1461-0248.2006.00900.x

Williams RJ, Martinez ND (2000) Simple rules yield complex food webs. Nature 404: 180-183.

Williams RJ, Martinez ND (2004) Stabilization of chaotic and non-permanent food-web dynamics. The European Physical Journal B-Condensed Matter and Complex Systems 38: 297-303.

Wilson DS (1975) The adequacy of body size as a niche difference. The American Naturalist 109: 769-784.

Woodward G, Hildrew AG (2002) Differential vulnerability of prey to an invading top predator: integrating field surveys and laboratory experiments. Ecological Entomology 27: 732-744.

Wootton JT, Emmerson M (2005) Measurement of Interaction Strength in Nature. Annual Reviews in Ecology and Systematics: 419-444.

Xia JY, Rabbinge R, Van Der Werf W (2003) Multistage Functional Responses in a Ladybeetle-Aphid System: Scaling up from the Laboratory to the Field. Environmental Entomology 32: 151-162.

Yodzis P, Innes S (1992) Body Size and Consumer-Resource Dynamics. American Naturalist 139: 1151-1175.

Young S, Watt PJ, Grover JP, Thomas D (1994) The unselfish swarm? Journal of Animal Ecology: 611–618.

Zhang R, Heong K, Domingo I (1996) Relationship between temperature and functional response in Cardiochiles philippinensis (Hymenoptera: Braconidae), a larval parasitoid of Cnaphalocrocis medinalis (Lepidoptera: Pyralidae). Environmental Entomology 25: 1321-1324.

Zhang Y, Zhang Z, Ji J, Lin JZ (1999) Predation of Amblyseius longispinosus (Acari: Phytoseiidae) on Schizotetranychus nanjingensis (Acari: Tetranychidae), a spider mite injurious to bamboo in Fujian, China. Systematic and Applied Acarology 4: 63-68.

Zhang Y, Zhang Z, Lin JZ, Liu QY (1998) Predation of Amblyseius longispinosus (Acari: Phytoseiidae) on Aponychus corpuzae (Acari: Tetranychidae). Systematic and Applied Acarology 3: 53-58.

4. Appendix

4.1. Curriculum vitae

Personalities

Name: Olivera Vucic-Pestic

Adress: Am Markt 12, 51143 Köln

Date of Birth: 10.10.1976, Frankfurt am Main (FFM)

School carrer

1983-1887	elementary school (Uhlandschule, FFM)
1987-1997	grammar school
1997	general qualification for university entrance (Abitur, Max-Beckmann Schule in FFM)

Scientific career

1997-2005	Student of biological sciences, University of Technology Darmstadt
2005-2006	Diploma thesis
2006	Diploma degree in Biological Sciences
2006-2010	PhD-thesis in Ecology on the topic “ Terrestrial Functional Responses “

4.2. Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig und nur mit den angegebenen Hilfsmitteln angefertigt habe.

Darmstadt, den 18. Januar 2010

Olivera Vucic-Pestic

4.3. Danksagungen

Ich danke meinem Vater Slobodan, der immer an mich geglaubt hat und mich immer unterstützt hat solange er da war.

Ich danke meiner Schwester Vesna, die immer für mich da ist und mir Freude, Rückhalt, Trost und Zuflucht spendet, wann immer ich Sie brauche.

Ich danke meiner Mutter Zagorka und meinem Stiefvater Obren für die Unterstützung und den Halt die sie mir immer entgegenbrachten. Ebenso meiner Tante Radmila und meinem Cousin Mirko, dafür das es sie gibt und sie immer an mich geglaubt haben.

Ich danke meinen Professoren Stefan Scheu und Ulrich Brose für die Unterstützung und Hilfe während meines Studiums und die freundschaftliche Arbeitsatmosphäre in ihren Arbeitsgruppen.

Ich danke meinen Freunden (die ich jetzt nicht alle im Einzelnen aufzählen möchte) für ihre Geduld, ihre Aufmunterungen, ihren Trost, also kurz für ihre Freundschaft. Danke das es euch gibt und das ihr so seid, wie ihr seid und mich so nehmt, wie ich bin.

Ganz besonders danke ich meiner guten Freundin Ellya, die immer uneingeschränkt für mich da war und auf die ich mich immer verlassen konnte, seit nunmehr schon zehn Jahren.

Ich danke Alex J., Sonia K., Roswitha B. E. für ihre Anregungen und fürs Korrekturlesen dieser Arbeit. Natürlich danke ich auch Björn C.R., meinem Computerdoc, ohne dessen Formatierhilfe und Untersterstützung beim Erstellen der Graphiken diese Arbeit bestimmt noch etwas länger gedauert hätte.

Ich danke Dora V. für ihr einzigartiges Organisationstalent, ihre Zuverlässigkeit und ihre Freundschaft.

Ich danke Petra H. für die Collembolen- und Drosophila-Zuchten, mit denen sie mir ein ums andere mal ausgeholfen hat, wenn meine Vorräte an Beuteorganismen mal wieder zu neige gingen, und ich danke allen Hiwis, die unzählige Stunden, Tage und Wochen mit mir im Labor gestanden haben und abertausende Springschwänze und Fruchtfliegen mit mir gezählt haben.

Ich danke allen Mitgliedern der AG Scheu und AG Brose für die immer währende Hilfsbereitschaft und das tolle Arbeitsklima.